ANATOMICAL AND AGRONOMIC STUDIES OF PHORMIUM IN WESTERN OREGON

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CONTENTS

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ANATOMICAL AND AGRONOMIC STUDIES OF PHORMIUM IN WESTERN OREGON

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SUMMARY AND CONCLUSIONS

A detailed study was conducted on the origin, growth, development, and structure of the vegetative organs, and the development of the flowers in *Phormium tenax* Forster.

Although the morphology and anatomy of phormium generally resemble that of other monocotyledons, this research provided the much-needed details about the structure and development of this fiber plant.

In order to complete the picture concerning phormium growth and development, reproduction studies were conducted on the flowering habit, pollen characters and pollination, stigma receptivity, and pollen germination and pollen tube growth of *P. tenax*. Investigations of flowering habit included heading period and order, process, time, and frequency of flower opening. Pollen characters studied were pollen identification, size, maturity, shedding, and dispersal. Stigma receptivity studies were limited to time and duration after anther exsertion. Pollen germination studies included conditions for germination on artificial medium, pollen longevity under storage, and agents of pollination.

The main conclusions of the reproduction studies were:

(1) In general, the heading period in western Oregon is from early May through early June.

(2) Flowering (the time when flowers open) occurs in June and usually ends in September. The flower-opening processes are positively associated with high temperature and low relative humidity.

(3) Pollen shedding begins shortly after flower opening, with dispersal occurring from early morning until evening. Greatest density of pollen in the air is during the period from midmorning to midafternoon.

(4) Self-pollination is inhibited by the proterandrous flowers in nature. Bees and humming birds are important agents in pollination; however, wind becomes an agent of pollination when the temperatures are high (about 20° C.) and relative humidity is low (35 to 40 percent).

Observations of ornamental plantings on the Pacific Coast of the United States showed that phormium might be grown in western Oregon as an emergency source of hard fiber or as a supplementary farm crop. Agronomic studies were

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directed toward gaining basic information on field production and adaptation of phormium. The main conclusions of the agronomic studies were:

(1) Phormium is well adapted to the Oregon Coast south of Honeyman State Park.

(2) Temperature appeared to be the limiting environmental factor in the adaptation of phormium in western Oregon.

(3) Fertile soil and adequate soil moisture through the summer favored the growth of phormium.

(4) Fertilization with nitrogen, phosphorus, and potassium, in all combinations, did not increase yield of leaves and fiber. However, phosphorus-potassium treatments lowered the percentage of fiber in green leaves.

(5) Higher yielding clones tend to be rather low in percentage of fiber.

(6) Results of plantings in other areas of Oregon suggest that coastal areas present the most favorable climatic conditions for high yield and quality of fiber.

Other details on cutting heights, cutting interval, and stand establishment were examined, and results would have bearing should phormium ever become an important commercial crop.

Conclusions of seed germination studies, including dormancy, stages of maturity at harvest, keeping quality, seedling vigor, and optimum germination conditions, were:

(1) Optimum temperatures for seed germination were alternations of 15° to 25° C. and 15° to 30° C. Rate of germination was very slow when seeds were held at constant temperatures.

(2) Seed maturity is very important in seed germination, keeping quality, and seedling vigor. No dormancy was present when seeds were harvested 50 to 90 days after anthesis. Immature seeds were very slow to germinate. Self-pollinated seeds showed decreased germinability.

INTRODUCTION

Phormium tenax Forster—commonly known as phormium, New Zealand flax, New Zealand hemp, or the Harakeke lily—is indigenous to the islands of New Zealand and the Norfolk Islands. *P. tenax*, along with *P. colensoi* Hook f. (mountain flax), was used for wearing apparel, fishing nets, baskets, mats, shoes, and twine by the aboriginal Maoris of New Zealand. Captain Cook, the English explorer, first discovered phormium and introduced it to Europe. Phormium was soon recognized as a source of fiber for the cordage industry, and phormium fiber was exported from New Zealand during the 19th century (*2*).[4] The fiber is slightly inferior in strength to abaca and sisal, but has been blended with these fibers or substituted for them for limited use (*1*).

Although a relatively minor fiber crop of the world, phormium is the only known hard-fiber plant that grows well in temperate climates. Phormium, therefore, may assume strategic importance for countries such as the United States that import their entire supply of hard fibers from tropical regions. Phormium was first introduced into the United States as an ornamental plant and little was known of its culture on a field scale or its growth and development under the environmental conditions of Oregon. Consequently, the U.S. Department of Agriculture in cooperation with the Oregon Agricultural Experi-

[4] Italic numbers in parentheses refer to Literature Cited, p. 42.

ment Station began research on phormium in 1949. Objectives were the determination of the range of adaptation, fertilizer response, harvesting methods, stand establishment, the selection of superior varieties, and seed germination and maturity. Later, in conjunction with the agronomic studies, research was begun on reproductive characters and the morphology and anatomy of the plant. The morphologic and anatomic studies covered the vegetative shoot apex, adventitious roots, maturation of tissues, origin of lateral roots, the development of the leaf, and a complete botanical description.

BOTANICAL DESCRIPTION

Phormium tenax (fig. 1) as described by Atkinson (*2*) has a short, upright shoot springing directly from the rather large rhizome, or rootstalk. The rhizome produces an abundance of adventitious roots that form a typical monocotyledonous root system that is usually shallow in the soil, although roots sometimes penetrate deeply. The equitant leaves on each branch are arranged in the form of a fan, which usually consists of about eight or more leaves with the youngest one in the center and the oldest at the outside. The leaves are very thick and coriaceous, flexible, 3 to 6 feet long, 2 to 5 inches broad, linear-ensiform, rigid at the base, erect, dull-green above, and silvery and glaucous below. Each leaf is folded along the midrib with the upper surface innermost; on the outermost surface the midrib forms a sharp keel along the back of the leaf. The midrib and margin are bordered with a red or orange line. The tip of the leaf is usually slit when mature.

The flower stalk grows from the center of the fan and dies after fruits have matured. The life of a particular shoot ends with its production of fruit, but the rootstalk sends forth branches that can develop into new flowering shoots. The inflorescence is a panicle with numerous dull-red flowers borne on the upper branches of the rachis. The flowerbuds are protected by large bracts that fall at the time the flower opens, or sometimes several days later. The flowers are usually 1 to 2.5 inches long with the six perianth segments connate in the lower part and nearly straight or lightly recurved at the tip. Six stamens are inserted at the base of the segments to form two whorls of three each. The filaments of the outer whorl are considerably longer than those of the inner one. The superior tricarpellary ovary possesses a simple style that is usually about the same length as the filaments of the inner whorl of stamens.

The fruit is a loculicidal capsule 4 to 8 inches long, erect or inclined, stout, and never twisted. At maturity it splits into three segments, each of which contain numerous shining, black, flattened seeds.

Phormium, a perennial monocotyledon, has been classified by most botanists as a genus in Liliaceae. However, Hutchinson (*14*) removed *Phormium*, *Yucca*, *Dracaena*, *Doryanthus*, and *Agave* from Liliaceae and established a new family, Agavaceae, primarily on the basis of the woody caudex, the xerophytic habit, and the presence of basal or terminal fibrous leaves. Morphologically, the genus *Phormium* is not closely related to other genera of Agavaceae, with the possible exception of *Doryanthus*, and possibly both of these genera should be removed from this family (*5*, *6*).

FIGURE 1.—Typical *Phormium tenax* experimental planting, Hyslop Agronomy Farm, Corvallis, Oreg.

MORPHOLOGY AND ANATOMY

Vegetative Shoot Apex

The vegetative shoot apex is elevated slightly at the tip of the upright rootstalk into a spherical dome 90 to 120 microns high and 150 to 175 microns broad above the latest formed leaf primordium. The organization of the apex can best be interpreted in terms of the modified tunica-corpus concept, which has been used effectively by Stants (*27*) for many monocotyledonous plants. The meristem is differentiated into two distinct zones of tunica and corpus. The corpus is further differentiated into three more or less distinct zones that consist of a group of corpus initial cells, a rib meristem, and a flank meristem.

The tunica typically consists of two layers (fig. 2.) Since cells of the outermost layer divide only by anticlinal divisions, this layer remains discrete throughout the ontogeny of the shoot. The cells of the second tunica layer divide only anticlinally at the summit of the apex, but occasional periclinal divisions occur on the flank just above the point of leaf initiation. The cells of both tunica layers over the summit of the apex are slightly larger, somewhat more vacuolate, and divide less frequently than those on the flanks of the apex and are considered to be tunica initial cells.

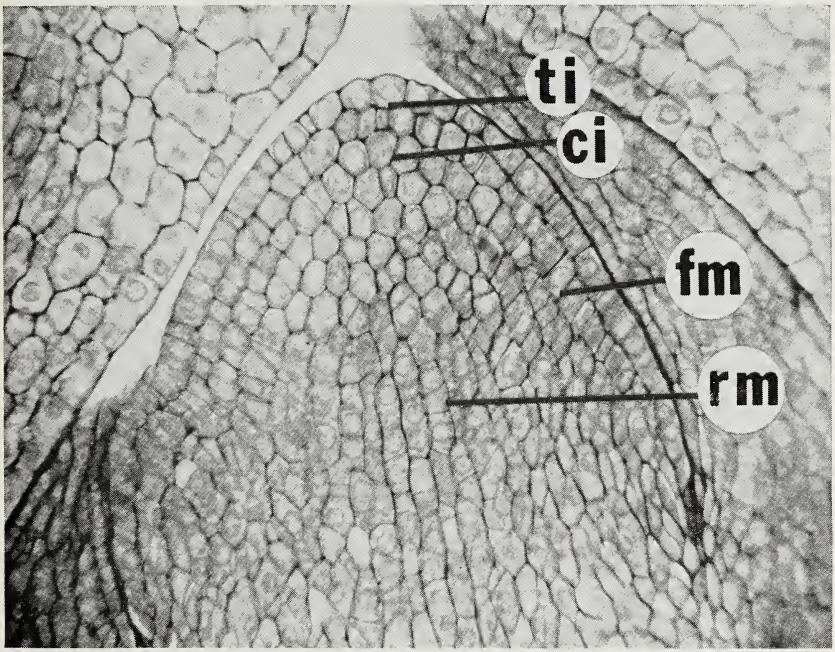

FIGURE 2.—Tunica initials (ti); corpus initials (ci); flank meristem (fm); rib meristem (rm).

Relatively inactive cells (in the region below the tunica initial cells) serve as corpus initial cells. They are larger than other cells of the corpus, somewhat more vacuolate, and have slightly larger nuclei. These cells divide rather infrequently by anticlinal divisions and

give rise to the rib and flank meristems. These meristems, together with the rapidly dividing cells of the tunica, form a cambiumlike concave zone of dividing cells across the apex about halfway between the summit and the latest formed leaf primordium. This zone is relatively distinct in a rapidly growing apex but much less so when the apex is dormant.

The rib meristem is less active in division than the flank meristem, and derivatives of the rib meristem elongate rapidly to form a distinct column in the base of the apex. Below the apex some periclinal divisions occur, and the cells enlarge so that rows of cells diverge outward and downward to form what is essentially a pith region in the center of the stem (fig. 2). This is very similar to the development described for *Washingtonia* (*3*).

The cells of the flank meristem divide only anticlinally except during leaf initiation. Additional divisions at the base of the apex shift to an oblique position so that rows of cells derived from the flank meristem also diverge outward and downward. The first procambium strands into the leaf primordia are differentiated from derivatives of cells in the inner portion of the flank meristem.

At the base of the apex and extending beneath the bases of the leaf primordia is a region of rather uniform parenchymatous tissue traversed by the first procambial strands of the young leaves. In the inner part of this region the cells differentiate a distinct meristematic layer, the primary thickening meristem (*3*, *17*). This thickening meristem appears very close to the apex, usually under the base of the last or next to the last leaf primordium (fig. 2). It consists of two to six layers of cells, each of which divides several times before the derivatives mature or in turn undergo division. Since there are no distinct and persistent initial cells, this is not a true cambium, but a stored meristem. The primary thickening meristem is continuous except for the areas immediately surrounding the large procambial strands derived from the flank meristem.

Since the primary thickening meristem is usually differentiated under the last leaf primordium in the rows of cells diverging downward and outward from the flank meristem, and since the cell divisions are periclinal, the primary thickening meristem is responsible for increase in length of the stem as well an increase in diameter. Internally the thickening meristem produces parenchyma and scattered vascular bundles of the central core of the stem. These bundles are mostly additional leaf traces and will be discussed further in the section on leaf development. The last vascular tissue produced is the peripheral network of bundles that connect with the smaller leaf traces and especially with adventitious roots (fig. 3).

The cells of a uniseriate layer located one to three cells outside the vascular network develop distinct Casparian strips characteristic of an endodermis. An endodermis is not distinguishable in older parts of the stem, however, because this layer, like the cells between it and the vascular tissue, develops uniformly thick walls with simple pits at maturity. Thus in older stems the central core of the vascular tissue is separated from the cortex by a ring of sclerenchyma tissue, which represents the last derivatives of the primary thickening meristem (fig. 3).

Externally, the thickening meristem adds cells to the cortex. In addition, there is a slow increase in thickness of the cortex due to occasional divisions of derivatives of the meristem. Thus the cortex, which is initially only a few cells in thickness, becomes many cells thick at

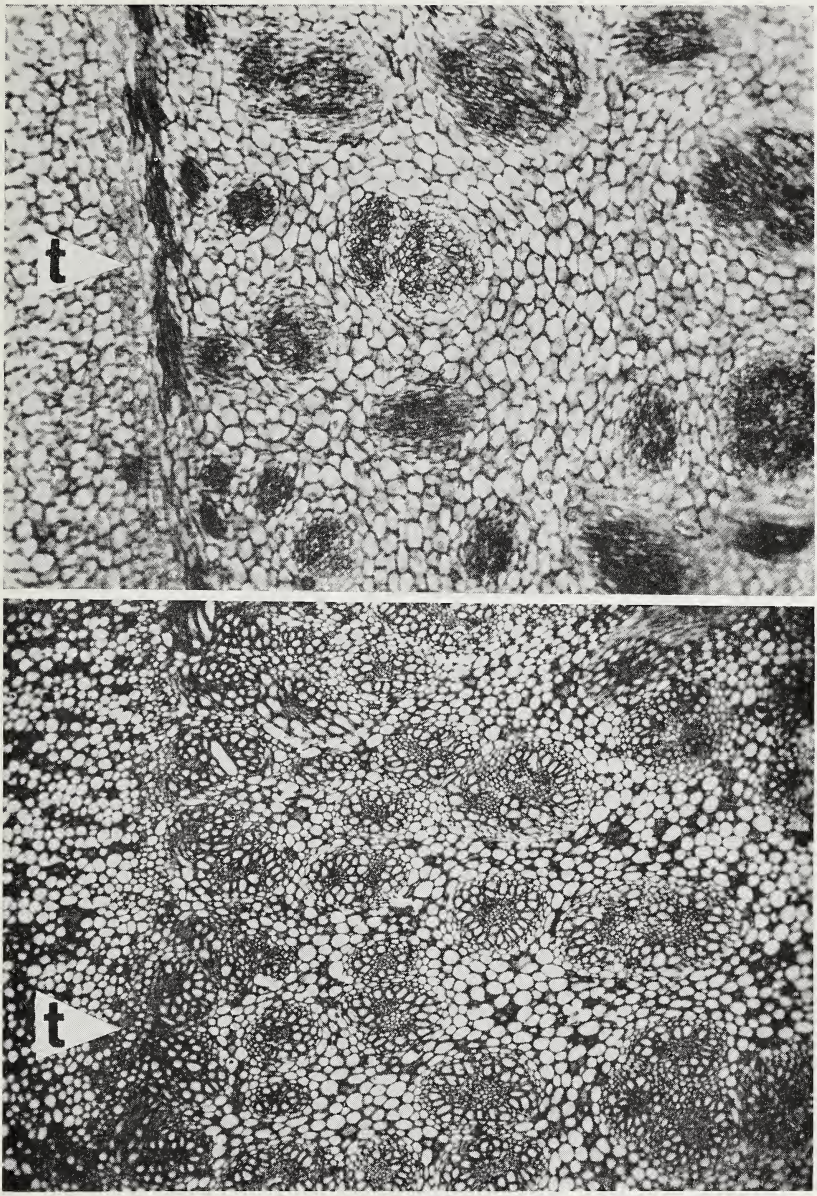

FIGURE 3.—(Top) Cross section of young stems shows the vascular network produced by thickening ring (t). Larger vascular bundles appear to be collateral bundles because metaxylem has not matured. (Bottom) Cross section of mature stem. Cells of the thickening ring (t) are matured and bundles are amphivasal.

maturity. It consists of parenchyma cells with numerous but small intercellular spaces. The outer cortical cells develop walls that are only slightly thicker than those of other cells in the cortex. The epidermal cell walls are moderately thickened at maturity and are covered with a thin cuticle.

The stem is covered almost completely by leaf bases. After the leaves die back to the base, storied cork develops inside the necrotic tissue. The development of storied cork then progresses to the very short internodal regions between the leaf bases. In these areas, the cells just beneath the epidermis divide first, and they may divide only once or twice before the derivatives differentiate into cork. Deeper cortical cells divide three to five times before differentiating into cork. Cork does not develop on any given portion of the stem until it is 3 to 5 years old, since storied cork formation is not initiated before the leaves die back.

The vascular tissue of the central core consists of two more or less separate groups of bundles, the peripheral bundles that branch freely and are interconnected and the internal bundles that are more or less scattered. These internal bundles show numerous branches but are not interconnected to the extent shown by the peripheral network of bundles.

The internal bundles are of two somewhat distinct types that differ in structure and origin. The largest bundles are those derived from the flank meristem and represent the first traces to the leaves. These quickly develop relatively large amounts of endarch protoxylem consisting of spiral elements that are mostly tracheids. Metaxylem initial cells do not become evident until much later. Thus in the upper part of the stem these large bundles appear to be collateral (fig. 3). At the level where adventitious roots are developing, metaxylem initial cells enlarge and gradually differentiate metaxylem elements external to and along the sides of the phloem and the bundles become amphivasal (fig. 3). The metaxylem elements are mostly tracheids (*7*) with opposite or scalariform pitting, but a few vessel elements with simple perforation plates have been observed.

The second type of internal bundles is also amphivasal but is smaller in diameter than those derived from the flank meristem and is derived from the primary thickening meristem. These bundles may be either anastamoses or smaller leaf traces. They differentiate much smaller amounts of protoxylem and at lower levels in the stem. In many of them, no spiral elements are differentiated and all xylem could be considered metaxylem. The xylem elements here are also mostly tracheids with opposite or scalariform pitting.

Both types of bundles at maturity are enclosed in a sheath of mechanical tissue that consists of elongated modified parenchyma cells with thickened walls and simple pits.

The vascular pattern in the stem is considered to be a modified palm type (*16*, *18*). Each large bundle in the base of the leaf extends inward and downward across the cortex through a gap in the peripheral network of vascular tissue into the central core where it follows an obliquely downward course almost to the center of the stem. Then it turns outward and downward in a broad curve and unites with the peripheral network.

Adventitious Roots

Adventitious roots of phormium originate in the primary thickening meristem as has been described in other monocotyledonous plants (*16*, *17*, *18*). At the level where these roots originate, approximately 1 centimeter from the tip of the

stem, the protoxylem and primary phloem of the larger vascular bundles in the stem are mature. The smaller strands and, particularly, the peripheral network still consist principally of procambium.

The first indication of root initiation is a series of periclinal divisions in the thickening meristem. Cells are produced both outside and inside so that the thickening meristem bulges outward in this area (fig. 4). Adjacent cells of the cortex also undergo division at this time but at a slower rate. An endodermis is not recognizable in the stem at this stage of development. A period of very rapid cell division follows during which cells in the center of the young root primordium—cells derived from the thickening meristem and from the cortex—divide both periclinally and anticlinally. The resultant pressure crushes the nondividing cells of the cortex adjacent to the primordium (fig. 4). The cells in the inner portion of the primordium enlarge, especially tangentially, and act as rib meristems to establish the central parenchyma region of the the young root (fig. 4).

Procambium differentiates acropetally from the strands of the peripheral network toward the as yet unorganized root initial cells (fig. 4). Extending laterally from the region where root initial cells will differentiate is a plate of cells that are smaller than adjacent cells, divide more frequently, and have denser cytoplasm. This plate is flat near the initial region and then curves slightly back toward the base of the primordium. Beyond this plate, which becomes the dermatogen, the cells enlarge, become more vacuolate, and differentiate the first rootcap (fig. 4).

After the rootcap is clearly differentiated, definite patterns of cell division are established, but there are as yet no obvious initial cells that can be associated with specific regions of the root (fig. 5). The initial region consists of a central core of cells that divide mostly periclinally. Some tiers of cells are continuous from the rootcap through the region of cell division into the central parenchymatous region of the root (figs. 4 and 5). Around the periphery of the core of periclinally dividing cells, the divisions shift to the anticlinal planes. These divisions establish the tiers of cells in the procambium, cortex, and epidermis. Procambium is differentiated to within a few cells of the initial region.

The thickness of the cortex is increased rapidly by periclinal divisions that may occur anywhere in the cortex but are much more frequent in the endodermal layer. The endodermis differentiated in the root becomes continuous with the endodermis in the stem. A distinct dermatogen is differentiated over the area where the cortex thickens most rapidly (fig. 4). Just ahead of the dermatogen, continuous tiers of cells may extend from the rootcap across the dermatogen region into the cortex. Numerous periclinal and some anticlinal divisions occur in all the innermost cells of the rootcap from the core of initial cells laterally into the area where the dermatogen is differentiated.

Adventitious roots penetrate the cortex and covering leaf bases by a combination of enzymatic activity and pressure. After the root has emerged, the initial cells become more restricted and a more or less distinct plate of plerome initial cells is established (figs. 5 and 6). External to this is a plate of initial cells that may be one to three cells in thickness, depending on rate of growth and state of activity at the time material was collected (fig. 5). Probably the initial cells in this region can produce at different times cells destined for the rootcap, dermatogen, or periblem.

The rootcap of either an adventi-

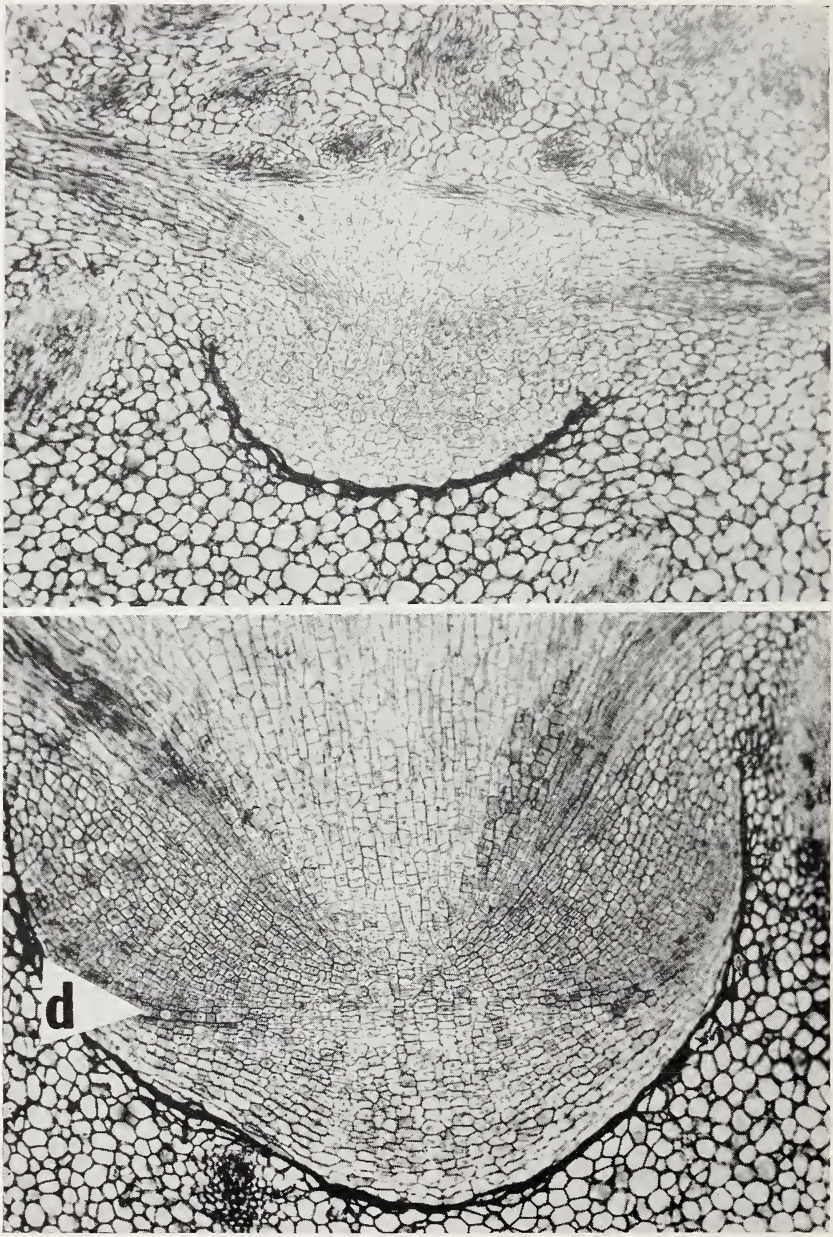

FIGURE 4.—(Top) Origin of adventitious root in primary thickening ring. (Bottom) Partly developed adventitious root within unorganized tiers of apical initials, definite rootcap, and dermatogen (d).

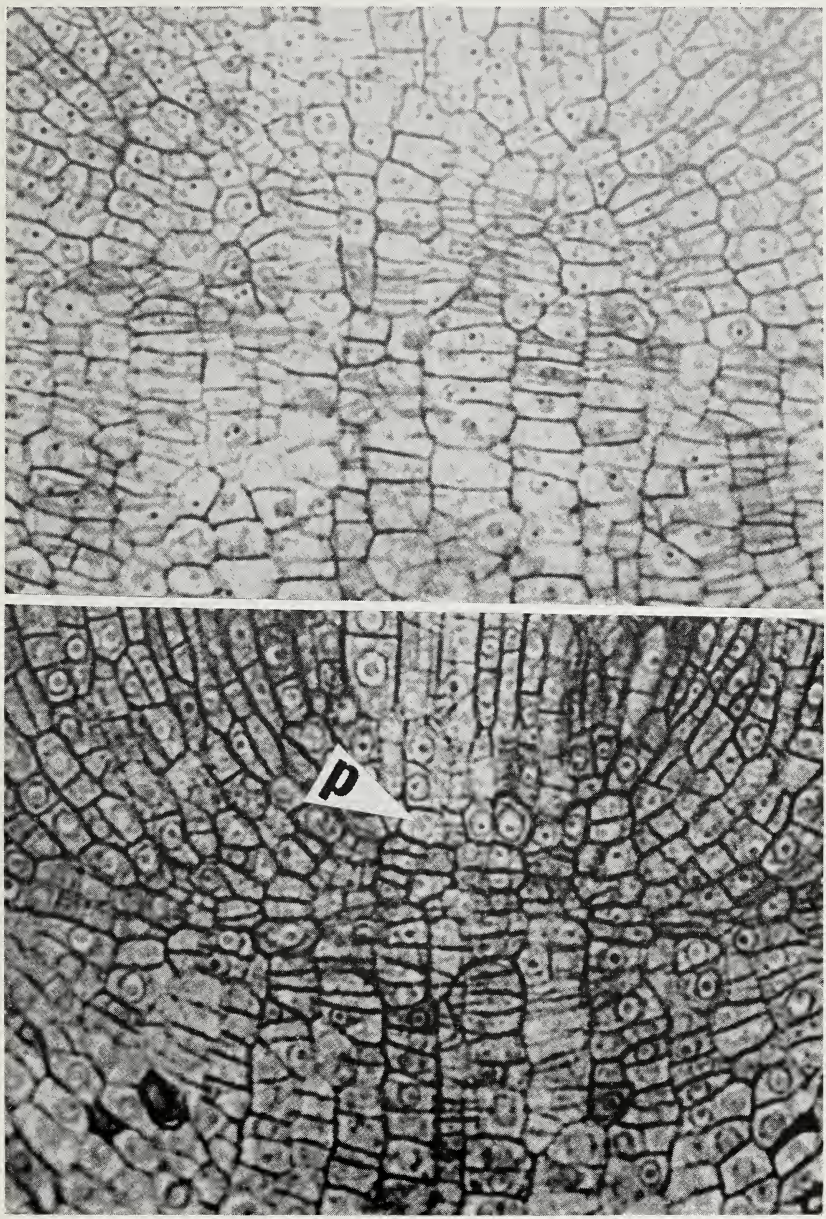

FIGURE 5.—(Top) Unorganized initial region in a partly developed adventitious root. (Bottom) Initials organized as plerome initials (p) and the indistinct plate of initials that produce the cortex, epidermis, and rootcap.

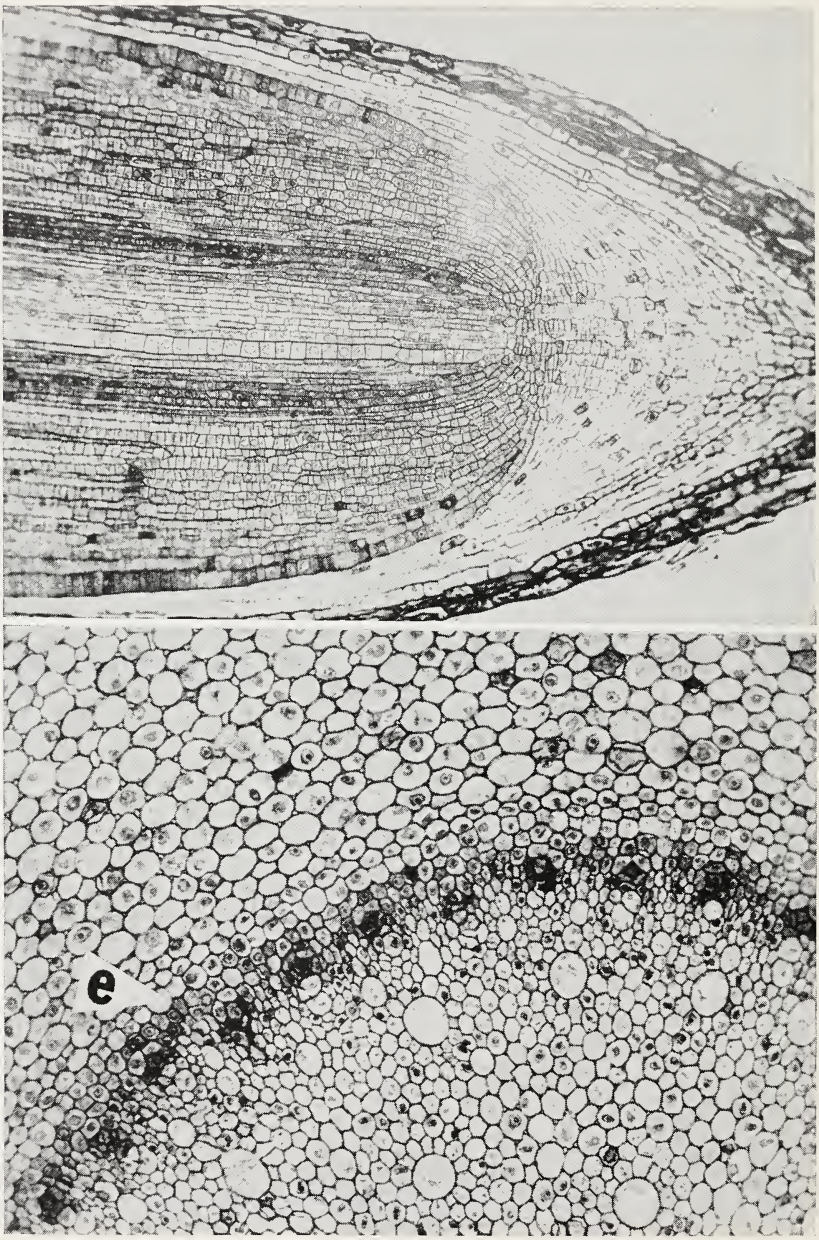

FIGURE 6.—(Top) Longitudinal section of apex of adventitious root. (Bottom) Cross section of adventitious root at level where protophloem elements are maturing. Endodermis (e) has not differentiated Casparian strips.

tious or lateral root contains a distinct column in which only periclinal divisions occur (fig. 6). The flanks of the rootcap are derived partly by periclinal divisions of cells adjacent to the dermatogen and partly by anticlinal divisions in cells adjacent to the column. The rootcap of an adventitious root is massive; it covers at least 1 centimeter of the root tip and is very mucilaginous.

Maturation of Tissues

Adventitious roots increase rapidly in length, and the primary tissues mature at relatively great distances from the initial cells. The tissues of lateral roots differentiate much closer to the apex. The first protophloem elements (fig. 6) in adventitious roots mature approximately 1.5 millimeters from the initial cells, but lateral roots frequently show mature protophloem at only 100 to 120 microns. In adventitious roots, the first protoxylem elements mature at approximately 1.5 centimeters from the apex, but the first metaxylem matures at 7 to 8 centimeters.

At the level in adventitious roots where the first protophloem elements are maturing, anticlinal divisions in the dermatogen have practically ceased. The young epidermal cells are very narrow and elongated perpendicular to the surface of the root. Occasional cell divisions are still occurring in the cortex, especially in the outer layers, and in the endodermal layer. Radial rows of cortical cells derived from the endodermal layer are evident near the stele, but they will become indistinct as the intercellular spaces enlarge. The pericycle, which originates as an uniseriate layer, is two or three cells thick at this level and divisions are continuing. Some of the metaxylem elements have enlarged, but others will not become evident until later.

Adventitious roots observed in this study produced few or no root hairs. Atkinson (*2*) reported that root hairs develop on horizontal adventitious roots in dry situations but not on deep roots. If root hairs are not produced, the epidermis tends to persist as small rectangular cells with thin walls (fig. 7). The cells are sloughed after 2 to 3 years.

The cortex becomes differentiated into three distinct regions: a hypodermis, a central region of thin walls and large air spaces, and an inner region of compact parenchyma (fig. 7). The hypodermis is the region where the latest cell divisions occur and consists of smaller cells with few intercellular spaces. The outermost layers become suberized 6 to 7 centimeters from the root tip where suberization starts in the subepidermal layer and progresses inward. At full maturity, the hypodermis consists of from 5 to 10 cell layers that give the brown color to mature roots. The hypodermal cells grade inwardly into large parenchyma cells with large air spaces that are partly intercellular and partly lysigenous. Frequently this area consists of radial plates of parenchyma separated by large lysigenous cavities. Toward the endodermis the cells again become smaller and more compactly arranged, and the inner tangential walls of cells adjacent to the endodermis are thickened at maturity.

The endodermis matures very slowly. The cells are square in cross section, vacuolate, and have only slightly developed Casparian strips at the level where the first metaxylem elements mature. At 10 to 20 centimeters from the tip, the radial, transverse, and inner tangential walls are thickened somewhat (fig. 7) as are the inner tangential walls of adjacent cortical cells. The walls of the latter cells do not increase much in thickness, but those of the endodermal cells

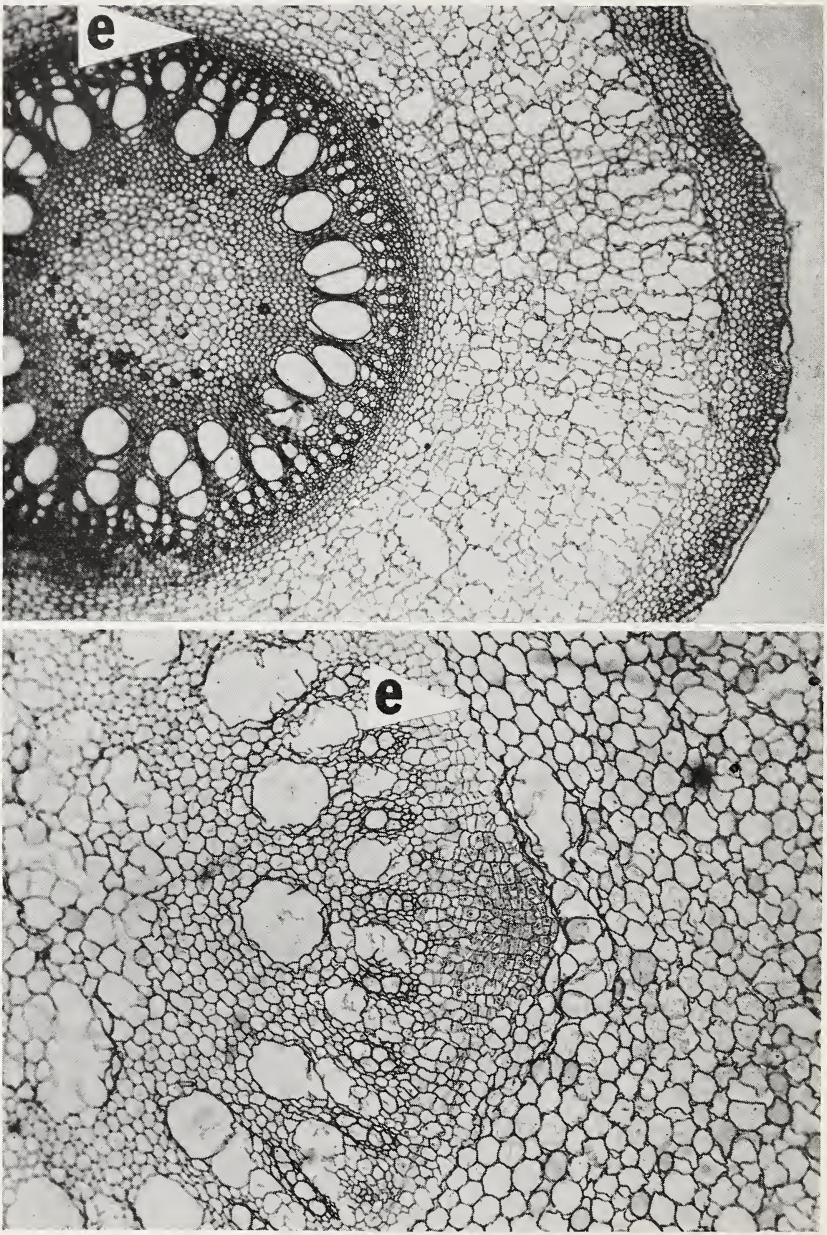

FIGURE 7.—(Top) Cross section of mature adventitious root showing persistent epidermis, thick hypodermal layer, air cavities in cortex, endodermis (e), and numerous protoxylem ridges. (Bottom) Origin of lateral root in pericycle and endodermis (e).

develop six or more lamellae and the lumen of each cell is reduced to less than half its former volume.

The pericycle becomes two to six cells thick because of periclinal divisions that occur in this layer up to 2 centimeters from the initial cells. These cells also develop thick walls, but at a slower rate than those of the endodermis.

Each phloem strand consists of two to six sieve tubes with associated companion cells. Neither protophloem nor the scalariform protoxylem elements are crushed at maturity. There may be from 25 to 75 protoxylem strands in adventitious roots and metaxylem elements differentiate in radial rows with each strand of protoxylem and also more or less separately in the central region of the root (figs. 6 and 7). These elements are mostly tracheids, but both porous and scalariform plates occur. The walls of metaxylem elements are very thin and have elongate pits. Parenchyma cells surrounding both protoxylem and metaxylem develop thick lignified cell walls.

The tissues of lateral roots mature much closer to the initial cells than do those of adventitious roots. The epidermis of a lateral root is usually lost early because of the development and subsequent death of numerous root hairs. There is relatively less cortical parenchyma in lateral roots and the smaller stele shows only 5 to 30 protoxylem strands. All or most of the central parenchyma cells develop thick walls.

Origin of Lateral Roots

Lateral roots originate from adventitious roots at the level where one to four protoxylem elements in each strand are mature. The endodermis at this level consists of thin-walled cells with very slightly developed Casparian strips. The first indication of root initiation is a series of periclinal divisions in the pericycle (fig. 7). The endodermis is pushed outward and its cells develop more cytoplasm and become less vacuolate. At this early stage there is also evidence of digestion of adjacent cortical cells. Cells of the endodermis then divide both periclinally and anticlinally. Cortical cells adjacent to the endodermis are usually crushed, but an occasional cell will persist and can become meristematic. These cells do not add significantly to the developing primordium.

Cell divisions continue in both pericycle and endodermis. The endodermis along the sides of the primordium soon loses its identity because of repeated divisions in this area. Over the tip of the primordium, however, cells derived from the endodermis soon differentiate the initial rootcap (fig. 8). Meanwhile, pericycle cells surrounding the point of origin of the primordium undergo periclinal divisions. Divisions then progress laterally around the root and for like distances upward and downward from the point of initiation. Procambium is then differentiated at the base of the primordium and develops progressively toward the lateral root tip (fig. 8) and also into the pericycle in all directions. Thus, when the base of the lateral root is matured, there are vascular connections to 15 to 20 protoxylem ridges and to a like number of phloem strands (fig. 8). The endodermis of the lateral root becomes continuous with the endodermis of the adventitious root, but the connection is irregular because of the early disruption of the latter by cell division.

The lateral root penetrates the cortex more by digestion than by pressure, and a large digestive pouch is usually present ahead of the lateral root tip. The initials of the lateral root are well established by the time the tip emerges from the cortex.

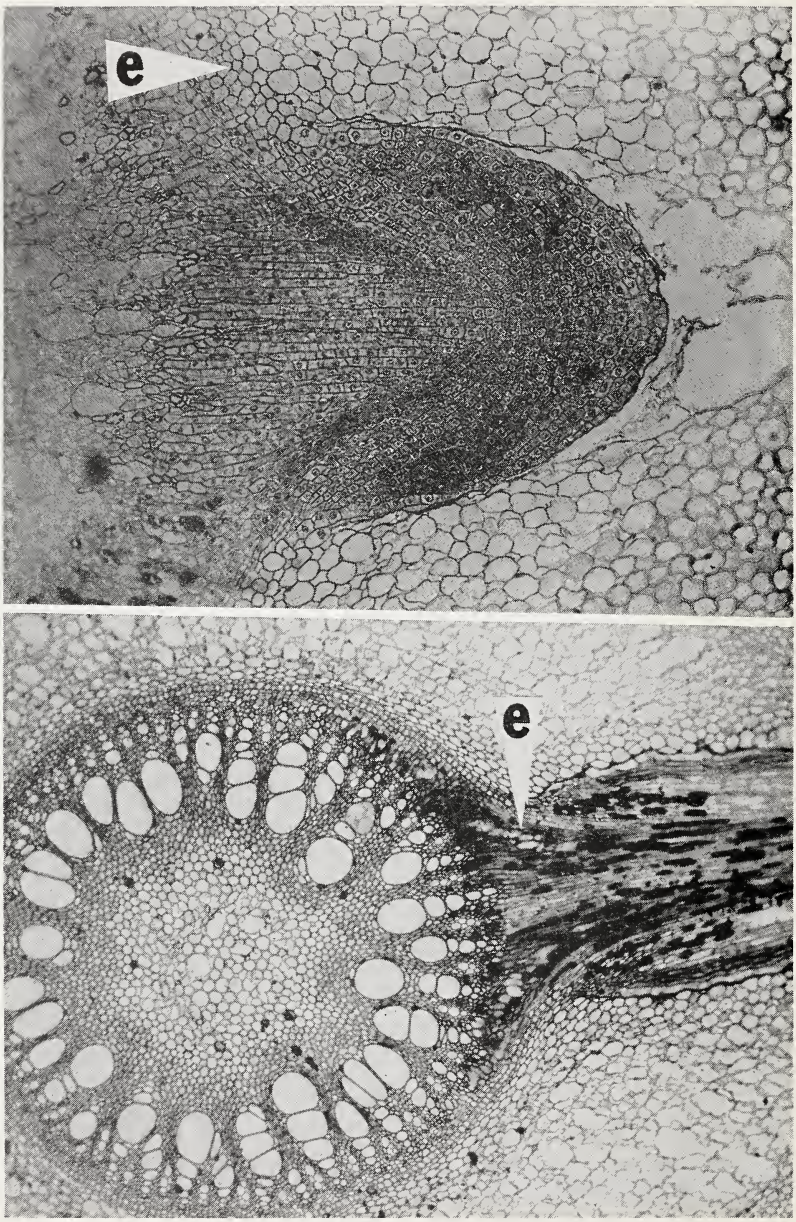

FIGURE 8.—(Top) Partly developed lateral root showing the initial rootcap derived largely from the endodermis (e), and digestive pouch in cortex. (Bottom) Cross section of adventitious root showing lateral spread of vascular connection with lateral root and continuity of endodermis (e) into lateral root.

Development of Leaf

Leaf primordia are initiated by periclinal divisions of cells in the outer corpus approximately 70 microns below the summit of the stem apex. This is just below the most active portion of the flank meristem. The periclinal divisions that initiate formation of the foliar buttress are at first restricted to a small area and involve only the third and fourth cell layers. Later both periclinal and anticlinal divisions occur, and the second tunica layer and deeper layers of the corpus become active. The initial periclinal divisions spread laterally around the stem, and continued growth results in the development of a crescent-shaped collar. The edges of this collar overlap on the side of the stem opposite the point of leaf initiation.

There is no real distinction between apical growth and marginal growth in the early development of the leaf since there is a row of dermal and subdermal initial cells along the entire crest of the collar. As the leaf increases in length, the initial cells at the highest point become less active and an intercalary meristem develops at the base. By the time the leaf is 2 to 4 millimeters tall, the intercalary meristem is primarily responsible for continued increase in length and soon becomes the only region of growth and persists at the base throughout most of the life of the leaf.

By the time increase in length is due primarily to intercalary growth, distinct marginal and submarginal initial cells are established. These initial cells are active for a long time (fig. 9) while the leaf and the stem to which it is attached increase in size. The marginal initial cell divides only anticlinally, but the submarginal initial cell divides either periclinally or anticlinally. Derivatives of the submarginal initial cell also divide in any plane so that parallel layers of anticlinally dividing cells such as occur in some monocotyledonous leaves (*20*) are not produced in phormium.

Indications of procambium differentiation appear early, but a definite procambium strand is not evident until the leaf primordium is 100 to 150 microns tall. At first there is only a single strand located at the center of the primordium (fig. 9). As expansion of the primordium continues, there is progressive lateral differentiation of additional procambium strands toward the margins. These strands are arranged in a single row, when seen in cross section (fig. 9), and will differentiate the large principal bundles of the leaf. They originate immediately below the young primordium in tissues derived from the flank meristem of the apex.

Smaller procambium strands are then differentiated centrifugally in tissues derived from the primary thickening meristem. These also appear first near the center of the leaf, where they are most numerous, and then laterally toward the margins. These strands are arranged approximately in rows between the abaxial surface and the principal bundles (fig. 9). The strands in each row become progressively smaller, and they are arranged approximately in an alternate manner in adjacent rows. These strands are differentiated downward and outward and connect with bundles in the periphery of the central core of vascular tissue.

Larger strands derived from the primary thickening meristem mature as collateral fibrovascular bundles in the leaf. These bundles alternate with the principal bundles derived from the apical meristem. Smaller strands mature as collateral bundles or as fiber bundles that contain neither xylem nor phloem. The fiber bundles develop from the

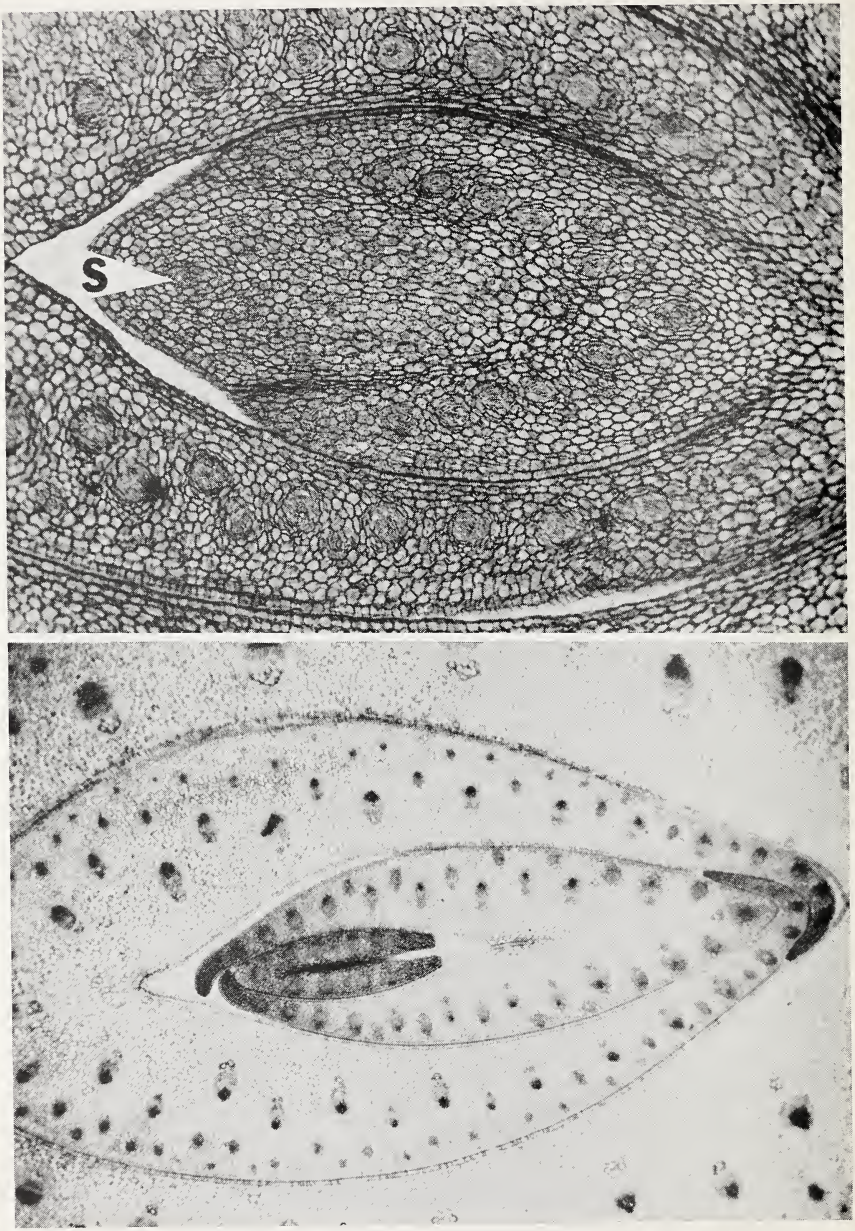

FIGURE 9.—Cross section just below apex showing the simple procambium strand (s) that first differentiates into leaf primordium and progressive differentiation of additional strands in older leaves. (Bottom) Cross section of young leaves showing marginal meristems.

last procambium strands that are differentiated for each leaf.

Thus, a cross section of the sheath of a mature leaf (fig. 10) will show several rows of bundles with more rows in and near the keel than in other parts of the leaf. The row nearest the adaxial surface consists of the first fibrovascular bundles derived from the primary thickening ring. The third row also usually consists of fibrovascular bundles, but some may be fiber bundles. Any additional bundles are usually fiber bundles that do not extend upward beyond the sheath. There are numerous, regularly arranged intercellular spaces in the parenchyma tissue of the sheath.

Through the sheath the parenchyma tissue gradually becomes more compact and the courses of the bundles shift so that they are more nearly in a single plane. There are always several rows of bundles in the keel, but in the rest of the leaf the arrangement becomes less obvious. The principal bundles are larger and the xylem is nearer the adaxial leaf surface (fig. 11). Alternating regularly with these are the first of the bundles derived from the primary thickening meristem. These are smaller and are located slightly toward the abaxial surface. Fibers associated with both of these types of bundles extend from the lower epidermis to the hypodermis above (fig. 11). Alternating with both of these types are strands from the second row of bundles derived from the thickening meristem. These bundles are extremely variable in different parts of the leaf. They may contain vascular tissue that is still more abaxially located and also fibers distributed as in the other bundles, or the bundle may be separated by parenchyma into a fiber bundle near the adaxial surface and a fibrovascular bundle below. In some cases, the bundle may consist only of a strand of fibers that is abaxially located, or it may become divided into two fiber strands, one of which is near the hypodermis and the other near the lower epidermis. Much larger fiber strands extend along the margins of the leaf and also are associated with the central bundle of the keel.

At approximately one-fourth to one-third of its length from the base, the leaf is tightly folded (fig. 10). A clear gum is present between the sheaths at the base and also between the closely appressed adaxial surfaces where the leaves are folded. Atkinson (*2*), in his detailed description of the structure of the mature leaf, states that in this area "there is actual coherence of their upper surfaces." Anatomically, this portion of the leaf might be considered as the upper part of the sheath. The principal bundles are nearer the adaxial surface, while all the secondary bundles are near the abaxial surface.

Stomata are mostly limited to the abaxial surface (fig. 11) and occur in longitudinal bands between the fibers. The cells of the lower epidermis, located just below the fibers, and all the cells of the upper epidermis are rectangular, elongated, parallel with the leaf axis, and have flattened or slightly convex outer surfaces. The protective layer between each cell lumen and the surface of the leaf consists of a much-thickened and cutinized outer cell wall and an equal thickness of cuticle. The epidermal cells in the strip where the sunken stomata are located have papillose projections. Plates of wax occur on both leaf surfaces, but around the papillose epidermal cells and near and in the stomatal openings are enough loose, granular wax particles to appear as a white bloom. Thus the upper epidermis is finely lined with alternate light and dark-green stripes, whereas the lower sur-

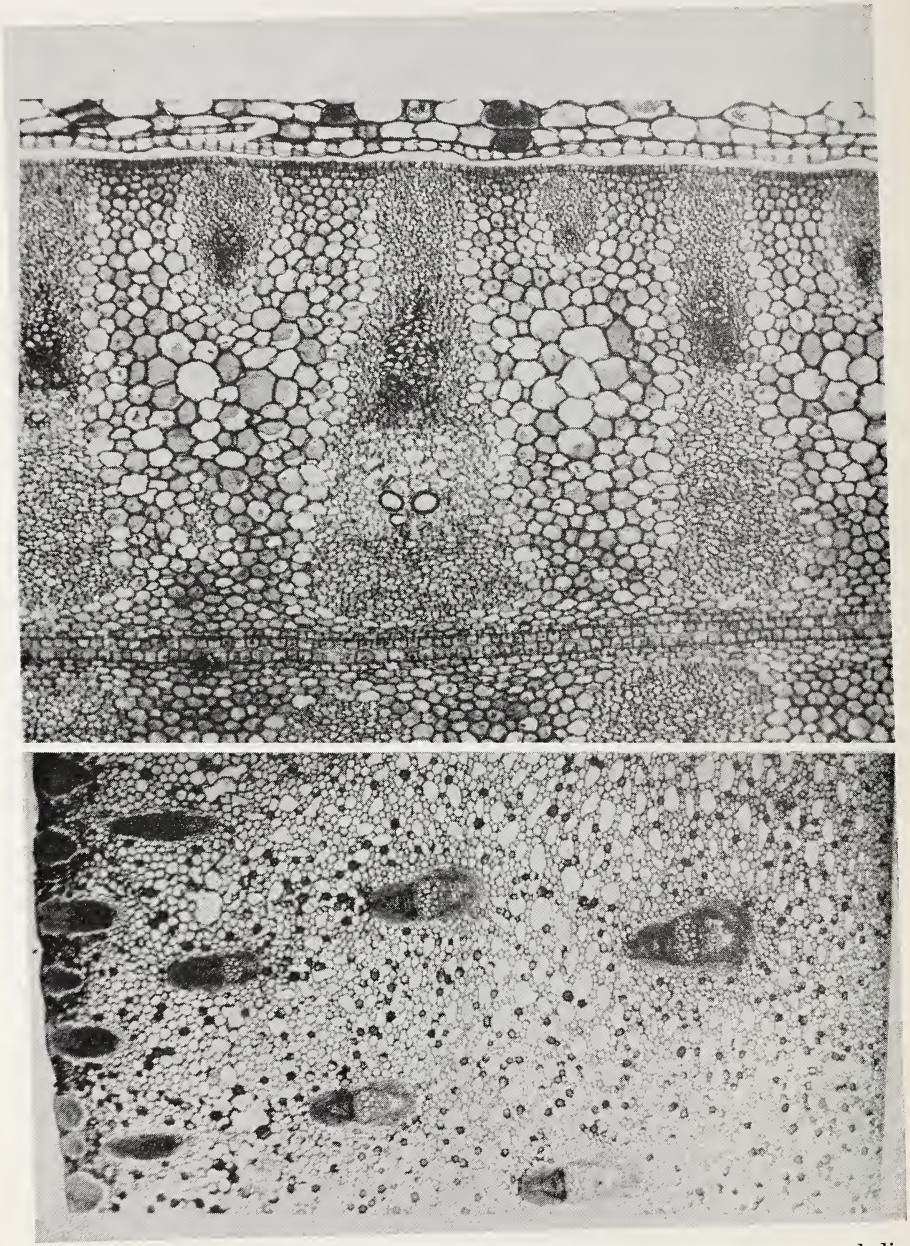

FIGURE 10.—(Top) Cross section of leaf sheath showing large air spaces and distribution of fibrovascular bundles. (Bottom) Cross section of young leaf where adaxial surfaces are folded together.

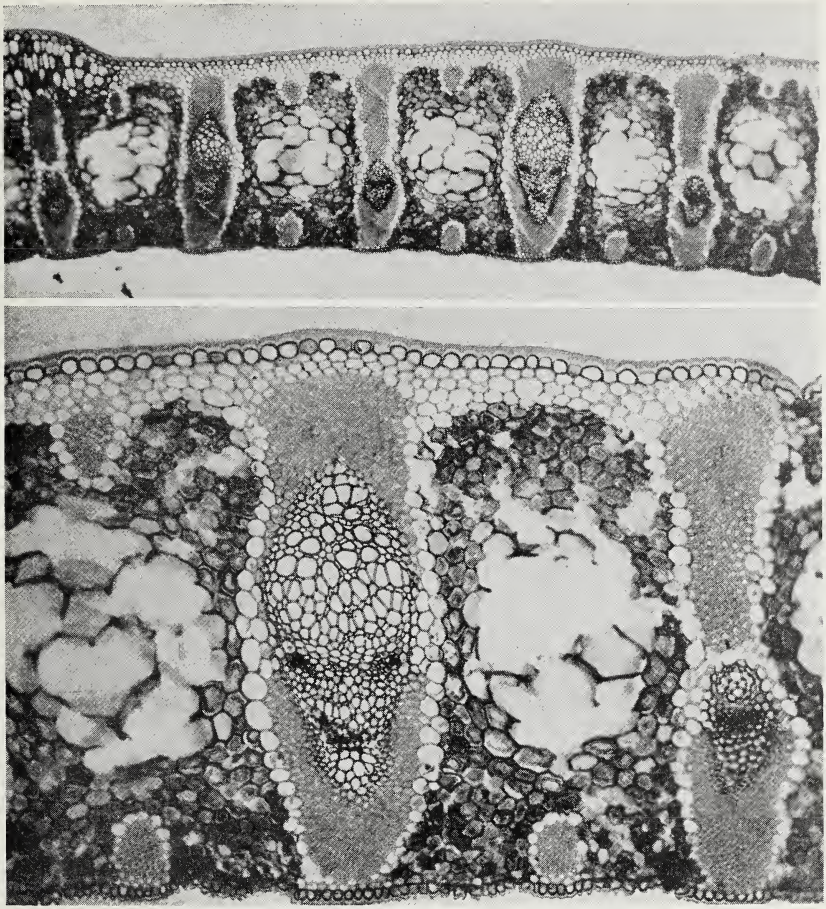

FIGURE 11.—(Top) Cross section of mature leaf showing distribution of fiber and fibrovascular bundles. (Bottom) Cross section of mature leaf.

face shows alternate white and dark-green lines.

The thickness of the layer that consists of the combined cuticle and cutinized walls of the epidermal cells varies greatly in different parts of the leaf. This layer is approximately twice as thick in the upper epidermis as in the lower. On both sides of the leaf, this layer is thicker on the expanded blade than on the sheath. The layer of the upper epidermis is thinner where the adaxial surfaces are closely appressed than where the blade is flat. The layer is much thicker over the midrib or keel and along the margins of the leaf.

There is a continuous hypodermal layer under the upper epidermis. The hypodermis is three or four cells thick and consists of cells with slightly thickened cell walls and no chloroplasts (fig. 11). Similar cells appear adjacent to the lower epidermis only where fiber or fibrovascular bundles are present. In both cases, the hypodermal cells merge with the border parenchyma that enclose all bundles with a sheath that is one or, rarely, two cells thick. There is no chloro-

phyll in any of the border parenchyma that enclose all bundles with a sheath that is one or, rarely, two cells thick. There is no chlorophyll in any of the border parenchyma cells.

In the center of the leaf between each pair of fibrovascular bundles is a longitudinal strand of large parenchyma cells that also lack chlorophyll. Chlorophyll occurs only in the smaller, compactly arranged cells surrounding these strands and in guard cells. The mesophyll cells containing chlorophyll are palisaded as seen in the longitudinal section of the leaf.

The structure of the fiber cells has been reviewed by Matthews and Mauersberger (*19*). The length and diameter of individual cells are extremely variable, but at least some of the variation is probably due to age of leaf, method of sampling, and environment. Fiber cells observed in this study were macerated from the middle portion of a 3- or 4-year-old leaf and varied from 0.48 to 1.25 centimeters in length and from 7 to 22 microns in diameter.

The fibers in a single fibrovascular bundle appear to be of two slightly different types. The fibers seldom completely encircle the vascular tissue but are arranged as two groups, one associated with the phloem and the other with the xylem. Those associated with the phloem are slightly smaller in diameter (fig. 11) and mature somewhat earlier (fig. 10). They develop fully thickened walls and rounded lumen at a time when the other fibers are still angular in cross section with the walls only half as thick as they will be at maturity. When both are fully matured, fibers associated with the phloem are smaller in diameter with slightly thicker walls and smaller lumens. The structure of the fibers in a fiber bundle varies with its position in the leaf. If the bundle is near the abaxial surface, the fibers resemble those associated with phloem. A fiber bundle near the adaxial surface consists of fibers like those associated with xylem. One Maori process of fiber preparation ruptures the fibrovascular bundle, and only the fibers associated with the xylem are used since these yield a softer and more pliable flax (*3*).

REPRODUCTION STUDIES

Flowering Habit

Smerle (*25*) reported that phormium propagated vegetatively in New Zealand flowered in the third year of its growth. A plant propagated by seed flowered in the fifth year after the seed was sown.

Time of heading and duration of blooming were observed in 1957 and 1958 at Corvallis, located in the Willamette Valley, and at Gold Beach and Brookings, located in the southwestern part of Oregon. Flower heads first appeared the last week in April at Gold Beach and the first or second week in May at Brookings and Corvallis. New flower heads appeared during May and early June. Flowering (the time when flowers opened) began in June at all three locations and continued into September at Gold Beach and Brookings, but ceased in July at Corvallis.

Average rate of growth of a flower stalk was 1.08 inches per day. The growth rate was higher in early stages of flower stalk development than in later stages.

Five flower stalks of the same age were selected from a block of well-established, clonally propagated plants at Gold Beach to determine the process of flowering. Each flower was tagged as soon as

it started to open, and was observed hourly from 5 a.m. to 8 p.m. for 4 days in June 1957.

During the first stage of flowering, the three outer perianth segments opened completely, whereas the three inner segments remained closed. During the next stage, the three inner segments separated, and the anthers began to exsert approximately 4 hours after flowering began. The anthers were completely exserted approximately 10 hours after flowering began. The anthers dehisced shortly after anther exsertion. At this stage, pollen grains were deep orange. Pollen grains started to turn yellow approximately 26 hours after flowering began and after 44 hours were completely yellow. The color of the pollen grains changed more rapidly when the temperature was high and the humidity was low. The stigma matured approximately 89 hours after flowering began. The stigma was swollen, white, and sticky at maturity.

Flowering started from the lowest part of the panicle and continued to the apex of the panicle. There was no definite order of blooming laterally on the panicle.

In order to study the time of flowering during the day, 20 nearly mature flower stalks of the same age were selected at Gold Beach on June 17, 1957, and 25 flower stalks were selected at Brookings on June 25, 1958. Counts were made each hour from 5 a.m. to 8 p.m. of the number of flowers in which the anthers had just begun to exsert. After each count, these flowers were tagged with the date and time of flowering. The time of flowering was recorded from June 17 to June 23, 1957, at Gold Beach, and from June 25 to June 30, 1958, at Brookings.

Temperature and relative humidity, as measured by psychrometers placed in the center of the field, were recorded hourly. General weather conditions such as the extent, duration, and time of cloudy or rainy periods were observed hourly.

The hourly rate of flowering was converted to hourly percent flowering on 20 plants in 1957 and 25 plants in 1958, on the basis of total number of flowers opened each day.

Flowering began at sunrise, and the maximum percentage of flowers opened from 7 a.m. to 9 a.m. (fig. 12). After 9 a.m., the frequency of flower opening declined. Generally a majority of flowers opened between 5 a.m. and 12 noon.

The 2 years' data indicated that flowering continued from sunrise to sunset with hour-to-hour and day-to-day fluctuations. Two peaks of flowering were observed, one at 8 a.m. and the other at 3 p.m. The afternoon peak was not as prominent as the morning peak. Flowering at Brookings in 1958 did not decrease in the afternoon as much as it did at Gold Beach in 1957. Trends of average hourly accumulative percentage of flowers opening in 1957 at Gold Beach and in 1958 at Brookings were quite similar.

Pollen Characters and Pollination

Cranwell (*9*) described the morphologic characters of pollen grains of *Phormium* sp. The pollen of *P. tenax* averaged 36 microns in greater diameter (34 by 36 by 30 microns), and pollen of *P. colensoi* averaged 30 to 32 microns in greater diameter. Atkinson (*2*), Hein (*13*), and Thompson (*28*) found that *Phormium* sp. flowers were pollinated mainly by insects and birds.

Twenty-five mature pollen grains were selected at random in 1957 and 1958 at Gold Beach and Brookings and in 1957 at Corvallis to determine variations in the size of pollen from year to year and location to location. Pollen was collected from the air on slides coated with vase-

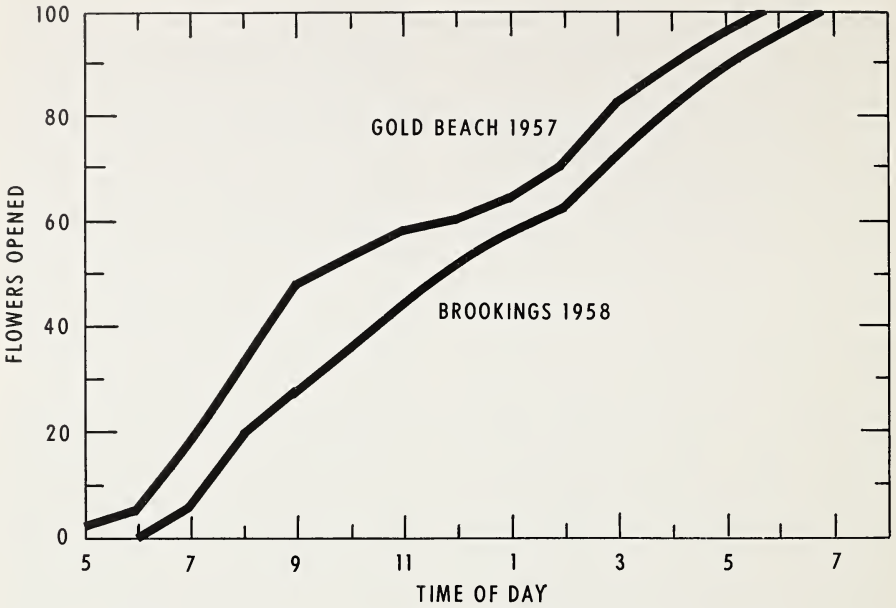

FIGURE 12.—Average hourly accumulative percentage of flowers opened in 1957 at Gold Beach and in 1958 at Brookings, Oreg.

line. Pollen grains were measured with the aid of an ocular micrometer. Results of tests for measuring pollen grains were as follows:

Location and year	*Average measurements (microns)*
Gold Beach:	
1957	34.51±2.6×34.65±2.42
1958	36.47±1.8×35.06±1.5
Brookings:	
1957	37.48±2.5×38.15±2.3
1958	36.68±2.4×35.19±2.9
Corvallis:	
1957	40.32±1.9×37.42±2.0
Total Average	36.1×37.1

Studies of the time of pollen shedding, pollen dispersal, and number of days that pollen was shed were conducted at Gold Beach in 1957 and 1958 and at Brookings in 1958.

Pollen shedding and dispersal were determined by exposing sets of vaseline-coated microscope slides attached to weather vanes at an angle of 45 degrees. Slides were exposed in the center of the field at heights of 4, 5, and approximately 6 feet (70 inches) to determine vertical dispersal of the pollen.

Temperature and relative humidity, wind velocity, and other weather conditions were recorded as for flowering records. (See above.)

The vaseline-coated slides were placed in the field at hourly intervals from 7 a.m. to 8 p.m. Some slides were left exposed from 9 p.m. until the following day (8 a.m.) to complete a 24-hour cycle. Following exposure for approximately 1 hour, all the pollen grains collected on a 1-square-inch area were counted under the microscope (×100). The average number of pollen grains caught at three heights was used for determining pollen-

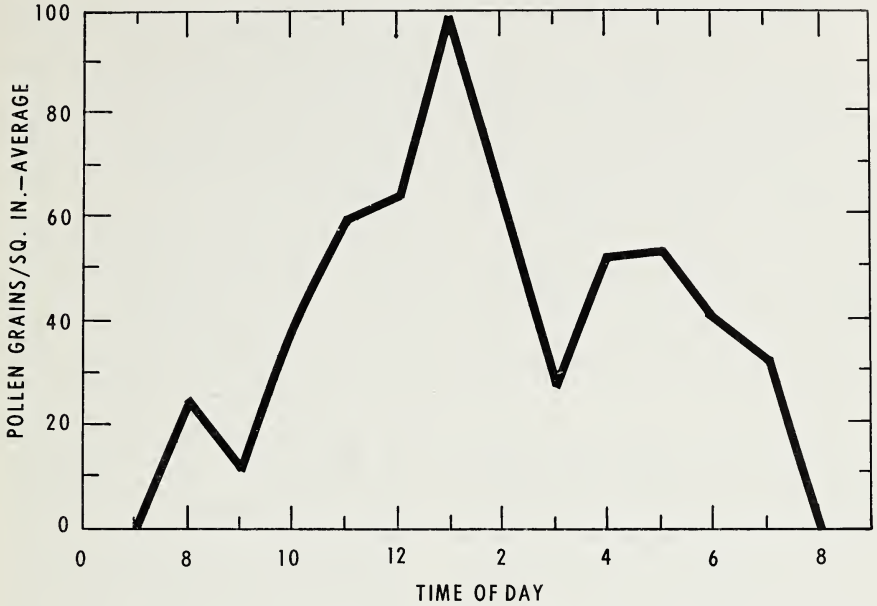

FIGURE 13.—Average number of pollen grains per hour (7 a.m. to 8 p.m.) collected in the center of *P. tenax* field in 1957 at Gold Beach, Oreg.

shedding data in 1957 at Gold Beach (fig. 13). The total number of pollen grains caught at three heights was used in 1958 at Brookings. Three slides were exposed at 8 feet at hourly intervals at Gold Beach in 1958, but only one of these was used for observation.

An attempt was made to determine the vertical and horizontal dispersal distances of pollen grains. Slides were exposed for 3 days for 24 hours at Brookings in June 1958 and for 1 day (9 hours) at Gold Beach in August 1958. Exposures were made at heights of 4, 8, and 12 feet. Exposure stations were established 10, 50, and 100 feet from the field on the windward side at Brookings, and 100 feet from the field on the windward side at Gold Beach.

Pollen shedding started at 8 a.m. and continued until 7 p.m. both years. Pollen shedding increased hourly and reached a peak at 1 p.m. in 1957, and at 4 p.m. in 1958. In the evening, orange pollen in clumps was collected on the slides both years. No pollen was collected after 7 p.m. No direct relationship was found between temperature, relative humidity, and pollen shedding.

Pollen shedding started shortly after flowering in June and continued until early September.

In 1957, pollen density was very high at Gold Beach because of a small honey bee population. In 1958, however, the population of bees increased at Gold Beach and was high at Brookings. As soon as the anthers dehisced, the bees collected orange, sticky pollen and left a small amount of pollen on the anthers. The pollen left on the anthers by the bees was later shed. Density of pollen grains, 100 feet from the phormium field, on the vaseline-coated slides placed at 12 feet was 4 pollen grains per square inch as compared to a density of 1 pollen grain per square inch on slides placed at 4 feet and at 8 feet.

Stigma Receptivity

Studies to determine the duration of receptivity of the stigma were conducted at Gold Beach in 1957 and 1958 and at Brookings in 1958. Flowers were emasculated at the beginning of anther exsertion, and each flower was covered with a paper bag to prevent cross-pollination. A set of five flowers, emasculated at one time, were hand pollinated at different intervals and the receptivity of the stigma was determined by the percentage of seed pod formation.

In 1957 at Gold Beach, the stigma was receptive 21 hours after the beginning of anther exsertion and continued to be receptive until 47 hours after exsertion. Stigmas were most receptive between 24 and 46 hours after the beginning of anther exsertion. At Brookings, stigmas were receptive 17 hours after the beginning of anther exsertion and continued to be receptive until 124 hours after exsertion.

Thirty-six and 24 percent of the flowers that were hand pollinated produced seeds at Gold Beach in 1957 and 1958, respectively. Only 5.6 percent produced seeds at Brookings in 1958.

Pollen Germination and Pollen Tube Growth

An experiment was conducted in 1958 at Corvallis to determine the effects of different levels of sugar, agar, and pH on pollen germination and pollen tube growth. Sugar (sucrose) solutions of 4, 6, 8, 10, 12, and 16 percent (by weight) were mixed with 1 percent agar (by weight), and the pH was adjusted to 6.3 ± 0.1 (table 1). Agar concentrations of 1, 2, 3, and 5 percent were used with 8 percent sugar and with a pH 6.3 ± 0.1. Pollen response to pH levels from 5.9 through 7.8 was determined in tests on a 1 percent agar and 8 percent sugar medium (table 2). The pH of the medium was adjusted before use with 1/20 normal hydrochloric acid (HCl) and sodium hydroxide (NaOH) and was not checked after the pollen germinated.

Pollen was dusted over the solidified medium on a microscope slide with a cotton swab, and clumps of pollen were separated with a camel's-hair brush. The slides were placed on wet paper toweling in covered petri dishes and incubated at 25° C. for 4 hours. After incubation, the dishes were transferred to a 0° C. temperature for 1 hour. Pollen-germination counts and tube-length measurements were then made.

Germination counts were made at random and a minimum of 250 pollen grains were counted. Pollen in clumps was counted only when 250 scattered pollen grains were not available. Two slides coated with each nutrient agar medium were used for each treatment, and half the pollen counts were made from each slide. Ten pollen tubes were measured at random on each of the two slides.

The best germination was obtained on 1 percent agar. As the agar concentration increased, the percentage germination decreased. The 8, 10, and 12 percent sugar concentrations appeared to be most suitable for pollen germination and tube growth (table 1). Swelling of pollen was observed at low sugar concentrations. As the time of incubation was prolonged, the swollen pollen burst without any growth. The pollen showed poor germination and tube growth at high sugar concentrations. Pollen tubes started to shrink at a sugar concentration of 14 percent.

Optimum pH for both percent germination and growth of pol-

TABLE 1.—*Effects of sugar concentration on phormium pollen germination and tube length (1 percent agar and pH 6.3±0.1)*

Sugar (percent)	Germination	Tube-length range		Average tube length
	Percent	*Microns*	*Microns*	*Microns*
4	34	98	534	304
6	28	80	650	312
8	66	374	917	540
10	62	312	1, 068	542
12	60	383	890	595
14	37	196	801	390
16	39	178	668	370

len tubes ranged from 5.9 to 6.5 (table 2).

When fresh pollen grains were dusted on the agar culture medium in dense colonies, the percentage of germination was high and the tubes grew very rapidly. However, when fresh pollen grains were dusted on the medium individually or in sparsely populated groups, they germinated within a few minutes, but the tubes grew slowly and there was less total tube growth.

Pollen development on the anther after dehiscence and its effect on germination were studied, using the vegetatively propagated (Wollam clone) *P. tenax* at Brookings in 1958. Four flowers were tagged as soon as they started to open and were covered with paper bags to protect pollen from honey bees. Anthers were collected 2, 4, 6, 12, 19, 22, 25, 27, 31, 49, and 58 hours after the flowers started to open. Anthers were cut and stored in glass vials lightly plugged with cotton. Immediately after all anthers were collected, pollen grains were germinated on a medium of 5 percent agar, 8 percent sugar, and distilled water, adjusted to pH 6.5±0.1. Pollen grains were counted and pollen tubes were measured as described above. Results are in table 3.

TABLE 2.—*Effects of pH levels on phormium pollen germination and tube length (1 percent agar and 8 percent sugar)*

pH	Germination	Tube-length range		Average tube length
	Percent	*Microns*	*Microns*	*Microns*
5.9	48	138	387	284
6.3	54	189	464	335
6.5	47	120	533	257
6.8	22	86	258	180
7.0	24	86	516	224
7.4	9	120	318	181
7.8	6	120	318	148

the southern area resulted in greater total accumulated growth. Fewer losses resulted from secondary effects, such as diseases, which are thought to follow cold injury. The high mean temperature in the southern area during the winter months promoted more winter growth and thus greater total accumulated growth there than in the northern coastal area. Other environmental factors such as soil, precipitation, and light may have caused differences in survival and growth between two or more locations, but they would not cause a progressive change over the entire range of the plantings, a north and south distance of approximately 220 miles.

More data would be required to definitely establish that Honeyman Park is the northern limit of the area in which no winter injury would be expected. Weather records (*29*) indicate that this limit probably should be farther south.

Fertilizer Response

Little experimental work has been reported on the requirements of phormium for mineral nutrients under varying soil conditions. Rigg and Watson (*23*) found phosphorus to be the most critical element on New Zealand podsol soils. Nitrogen and potassium had little effect on growth unless applied with phosphorus. Addition of lime to soil that had an initial pH of 4.4 did not increase growth. Berend (*4*) believed that lime and phosphorus were desirable for the growth of phormium on the Natal Coast. Dewey (*11*) stated that native stands of phormium were found on soils rich in nitrogen. Webber [5] reported from California that no growth differences were apparent among plants treated with nitrogen, phosphorus, or potassium when these elements were added at a low rate.

An experiment was begun in November 1954 to determine the effects of the application of 40 pounds of nitrogen, 80 pounds of phosphorus, and 80 pounds of potassium per acre, individually and in all combinations, on the yield, percentage of fiber in the dry weight, and strength of fiber of phormium in the nursery near Ophir. The experimental design was a split plot with three clones superimposed at random on the eight fertilizer treatments with two replications. Plants were spaced 5 feet between rows and 4 feet within the row. Fertilizer elements were supplied as ammonium nitrate, superphosphate, and potassium chloride. Five annual applications of fertilizer were broadcast around each plant in the plots receiving fertilizer treatments.

A sample of unfertilized soil from the experimental site was analyzed by the Oregon State University Soil Testing Laboratory. The test showed 9 pounds of available phosphorus and 172 pounds of available potassium per acre furrow slice, and a pH of 5.9. The soil of the site was somewhat heterogeneous after an overwash of sand during a flood.

Plots were harvested in September 1958. Leaf samples were taken to determine moisture and fiber percentages. One fan was selected from near the center of each plant and one from near the periphery. A large leaf in the second position laterally from the center immature leaf of each fan was cut at a height of 12 inches for moisture percentage determinations. Large leaves in the first and third positions laterally on the same side of the fan were cut at a height of 12 inches for fiber percentage determinations. The sample leaves were weighed immediately after cutting. All the other leaves of each plant were cut at a height of 12 inches, weighed in the

[5] WEBBER, J. M. Crops Research Division, Agricultural Research Service, U.S. Department of Agriculture, Berkeley, Calif. 1955. [Unpublished data.]

field to determine total yield of green leaves (green weight) for each plot, and then discarded.

Leaves for moisture determinations were dried artificially and weighed. Moisture percentages were used to calculate the dry weight of the harvested plants.

Leaves for fiber percentage determinations were first put through a Wakely Stripper to remove nonfibrous material from the green leaves. Fiber samples were washed, dried, and run through a small scutching machine to remove any adhering leaf tissues. Samples were then placed in an atmospheric conditioning chamber maintained at a dry-bulb temperature of approximately 85° F. and a wet-bulb temperature of approximately 70°. Samples were weighed within the chamber after equilibrium weight was attained, and fiber percentages in the green leaves were calculated. Total green weight as recorded in the field was multiplied by the fiber percentage to determine the fiber yield. Dry-weight percentages of fiber for each treatment were computed, and these data were transformed to angles to facilitate statistical analysis.

Fiber strengths were determined from the fiber samples at the Fiber Laboratory of the Agricultural Research Service, U.S. Department of Agriculture, Beltsville, Md., by methods outlined by Schiefer (*24*). Briefly, the tests consisted of preparing subsamples of fiber from the single leaf samples submitted to the laboratory, and obtaining breaking strength and elongation data by a pendulum-type testing machine. Subsequently, the breaking length of the bundles or samples, the length that would be just sufficient to break it under its own weight, was computed from the breaking strength and bundle weight and length.

No significant differences were found among fiber yields in response to fertilizer treatments (table 5). However, a significant decrease in percentage of fiber in dry leaves was found in plants treated with potassium (7.2 percent lower than plants in the check plots).

TABLE 5.—*Effect of fertilizer treatments on phormium fiber yield and fiber in dry weight after 46 months of growth at Ophir, Oreg.*

Fertilizer treatment	Fiber yield	Fiber in dry weight
	Pounds per acre	*Percent*
PK	10,041	60.8
NPK	8,168	59.6
Potassium	7,209	57.8
Phosphorus	6,730	62.3
Check	6,316	65.0
NP	5,968	60.2
NK	4,291	69.0
Nitrogen	3,528	66.8
LSD 0.05	NS	5.8

Clones showed significant differences in fiber yield and percentages of fiber in dry weight, irrespective of fertilizer treatments (table 6).

Results of yield responses of the fertilizer trial were inconclusive. Yield differences of the magnitude observed would probably have been significant if plants had been grown in a homogeneous soil and if a more efficient experimental design had been used. The relatively low amounts of available phosphorus and potassium in the soil suggest that differences in yields in response to these fertilizers could be expected. On the other hand, results suggest that differences in yield among clones might normally be greater than differences caused by the addition of fertilizers.

Irrespective of fertilizer treatments of clones, leaf 1 (the younger leaf) was found to be stronger than leaf 3 in strength-length to break and in knot strength (table 7). Differences in strength-length to break of fiber among fertilizer treat-

ments and among clones were not significant. However, nitrogen-phosphorus and phosphorus fertilizer treatments cause a significant increase in knot strength (table 7).

Logically, the reliability of the strength determinations was probably affected by the same factors that affected yield responses. The only consistent difference was that leaf 1 was stronger than leaf 3 in both strength tests. This strength difference probably would not be too important in commercial production since the average life of a leaf is not much over 2 years; thus, a harvest would not contain a preponderance of older leaves.

TABLE 6.—*Effect of clone selections on phormium fiber yield and fiber in dry weight after 46 months of growth at Ophir, Oreg.*

Clone selections	Fiber yield	Rank [1]	Fiber in dry weight	Rank [1]
	Pounds per acre		*Percent*	
P4–1–12	2,069	B	66.4	A
P6–2–6	8,015	A	60.2	B
P2–1–17	9,518	A	61.9	AB

[1] Duncan's Multiple Range Test, $P=0.05$. Selections with same letters are not significantly different.

TABLE 7.—*Effect of fertilizer treatments, clones, and leaf age on phormium fiber strength and knot strength*

Item	Strength-length to break	Knot strength-length to break
	Thousands of feet	*Thousands of feet*
Fertilizer:		
Nitrogen	85.1	26.4
Phosphorus	93.3	28.7
Potassium	87.9	25.5
NP	91.9	27.3
NK	83.9	26.1
PK	92.1	26.6
NPK	88.6	25.4
Check	89.3	26.2
L.S.D. at 5-percent level	NS	1.0
L.S.D. at 1-percent level		1.4
Clone:		
P4–1–12	86.2	25.7
P2–1–17	92.6	27.2
P6–2–6	88.3	26.7
L.S.D. at 5-percent level	NS	NS
Leaf age:		
Leaf 1 (younger)	93.7	27.2
Leaf 3	84.3	25.8

Harvesting Methods

The optimum height of cutting leaves was reported to be 6 to 8 inches above their insertion into the rootstalk. The optimum time interval between planting and first harvest varied from 4 to 6 years for a division planting, and from 6 to 8 years for a seedling planting. Intervals of 2 to 6 years, depending on soil and climate, were suggested as optimum between subsequent harvests (*2*, *10*, *22*). Jackson (*15*) stated that in Kenya, under selective cutting practices in which only the mature leaves were cut, a harvest could be made in 2 or 2½ years from time of planting.

An experiment was designed to study the effects of height and cutting interval on the yield and longevity of an established stand of phormium at Brookings. A split-plot design with three replications was used with plant spacing 6 feet by 6 feet. Cutting heights of 4, 8, and 16 inches were superimposed at random on 2-, 3-, and 4-year cutting intervals. Each subplot contained two plants. All leaves were first cut at the prescribed heights in September 1955. Leaves cut at a 2-year interval were again harvested in 1957 and in 1959, those cut at a 3-year interval in 1958, and those cut at a 4-year interval in 1959. Green leaf weights were recorded in the field. Four specific single-leaf samples were obtained from each plant at each harvest, except for the 2-year cutting interval in 1957, to determine fiber percentages and fiber yields. Data on fiber percentage in other cutting intervals indicated that the percentage of fiber in the green leaves for the 2-year interval in 1957 would be the average of the fiber percentage values of the 3-year interval and the 2-year interval in 1959. For purposes of average annual analysis, yield for each interval of cutting was calculated by dividing total yield by the number of years of growth.

Commercial fiber-stripping machines in common use outside the United States will not process leaves shorter than 3 feet. Consequently, the leaves in each plot in the 1955, 1958, and 1959 harvests were arbitrarily divided and weighed into two groups: leaves over 3 feet long and leaves under 3 feet long. The average percentage of the total green weight made up of short leaves was computed.

Total fiber yields on the basis of cutting intervals were found to be significantly different (table 8). Plants cut at 3- and 4-year inter-

TABLE 8.—*Effects of cutting height and cutting intervals on total phormium fiber yields, Brookings, Oreg.*

Cutting height (inches)	Fiber yield at—			
	2-year interval	3-year interval	4-year interval	Mean
	Pounds per acre	*Pounds per acre*	*Pounds per acre*	*Pounds per acre*
4	3, 473	7, 333	7, 442	6, 086
8	5, 421	7, 139	8, 155	6, 909
16	5, 808	6, 594	6, 316	6, 244
Mean	5, 022	7, 030	7, 296	
Rank [1]	B	A	A	

[1] Duncan's Multiple Range Test, $P=0.05$.

vals yielded more fiber than those cut at a 2-year interval. Plants cut at a 4-year interval would appear to outyield those cut at a 3-year interval in long green leaves (table 9); thus, 4 years seems to be the optimum cutting interval under the conditions of this experiment. Although cutting heights did not significantly affect the yield of fiber in the first harvest, they probably would have done so in several more cycles of cutting. Decreased yields (table 8) and an increased percentage of short leaves (table 9) were observed in the 4-inch cutting at the 2-year interval. The yields of plants cut at 3- and 4-year intervals at the 4-inch height of cutting would probably be adversely affected with continued harvesting. Thus, optimum cutting height would probably be between 8 and 16 inches.

Stand Establishment

Phormium is usually propagated asexually to maintain genetic purity since great variability exists in seedling populations. The Maoris planted four divisions together. Each division had leaves and roots. This method, or some modification of it, has been the normal practice in New Zealand to the present time.

In New Zealand, both fall and spring planting have been advocated, with 6 to 8 feet between plants and between rows. New plantings have been cultivated periodically for 18 to 20 months (*2*, *10*). In Africa and Brazil, seedlings have been preferred for planting, probably because of a greater tendency for stooling (*1*, *15*).

An experiment consisting of six treatments in a randomized block design with three replications was

TABLE 9.—*Effects of cutting height and cutting interval on percentage of total green leaf weight of phormium leaves less than 3 feet long, Brookings, Oreg.*

Cutting height (inches)	Total green weight at—			
	1-year interval	2-year interval	3-year interval	4-year interval
	Percent	*Percent*	*Percent*	*Percent*
4	8. 51	2. 14	1. 80	0. 74
8	9. 27	7. 28	. 80	1. 00
16	12. 69	8. 43	1. 10	1. 56

established in June 1956, at the Coquille nursery to determine the effects of the size and number of fans planted per hill on the establishment of a stand of phormium. The treatments were: (1) one small fan, (2) one large fan, (3) two united fans, (4) two single fans, (5) three single fans, and (6) three united fans. Each plot consisted of three hills, and hill spacing was 6 feet by 6 feet.

The plants were cut in May 1959 at a height of 8 inches and weighed in the field to obtain total yields of green leaves. Leaves were not graded into short and long classes. A sample of six whole leaves was taken from each plant at harvest to determine the fiber percentage and fiber yields.

Hills composed of three united fans were highest in fiber yield (table 10); hills composed of multiple fans were superior. However, results were based on only one harvest after 3 years' growth; differences in growth and vigor between

TABLE 10.—*Effects of stand establishment on phormium fiber yield and hill survival, Coquille, Oreg.*

Treatment	Fiber yield	Rank [1]	Hill survival
	Pounds per acre		*Percent*
One small fan	1,383	C	66
One large fan	1,844	C	66
Two united fans	3,719	B	89
Two single fans	3,990	B	100
Three single fans	4,323	AB	100
Three united fans	5,656	A	100

[1] Duncan's Multiple Range Test, $P=0.05$. Treatments with same letters are not significantly different.

treatments could diminish as the plants matured. In addition, the extra cost of planting stock and extra labor involved in planting multiple-fan hills might offset any increase in the yield from these hills.

Variety Trials

Selection of phormium began with the Maoris and was continued later by growers in New Zealand. In recent years, some further breeding and selection work has been done (*30*).[6] Selections of introduced New Zealand varieties (table 11) were evaluated at nurseries at Medford, Coquille, and Camp Adair. The Medford trial was planted in April 1954 and harvested in September 1958. The Coquille and Camp Adair trials were planted in June 1956 and harvested in September 1958.

The Medford trial was a randomized-block design with four replications. Each plot consisted of 10 plants and the spacing was 6 by 4 feet. Yields of green leaves were obtained by cutting the plants at a height of 12 inches and weighing them in the field. Four leaves were taken from each plant at harvest to determine fiber percentage in the green leaves or fiber yield.

[6] Also, BOYCE, W. R. Dept. Scientific and Industrial Research, New Zealand. 1959. [Personal correspondence with E. G. Nelson, U.S. Department of Agriculture, Beltsville, Md.]

TABLE 11.—*Phormium selections from New Zealand included in variety trials at Medford, Coquille, and Camp Adair, Oreg.*

Plant Introduction No.	New Zealand variety	Selection No.
183273	311	P1–2–5, P1–G, P1–1–2, P1–2–3, P1–2–13
183274	SS(S_3)	P2–2–13, P2–4–3, P2–3–1, P2–3–13, P2–3–15, P2–1–13.
183275	56	P5–1–1
183276	301	P6–2–1, P6–3–1, P6–3–5, P6–3–17, P6–4–9
183277	P4 [1]	P4–1–3, P4–4–1, P4–4–19, P4–4–17, P4–1–14, P4–3–3.
183278	SS	P3–1–17, P3–1–18, P3–1–14, P3–1–5

[1] *P. tenax* × *P. colensoi.*

Trials at Coquille and Camp Adair were randomized-block designs with three and four replications, respectively. Each plot consisted of one plant. A yield index was used to evaluate the potential yield of varietal selections since the leaves could not be harvested in the usual manner. Data were collected on the average height of the tallest leaves and on the number of fans; yield indexes were computed by multiplying average leaf height by the average number of fans.

A significant difference in yield indexes was found among the selections from the New Zealand varieties in each of the three trials (table 12). One example is the Coquille trial in which P4–3–3 was the highest yielding selection and P4–1–3 was the lowest. These differences emphasized the heterozygosity of the New Zealand varieties and pointed out the need for selection and plant breeding to obtain high-yielding, well-adapted plants. Fiber yield and quality were not determined in these tests.

The adaptation study revealed that phormium in the Medford area, which is inland and mountainous, was frequently damaged by low winter temperatures and did not yield as well as phormium along the southern Oregon coast. Hence the Medford variety trial was not very useful for testing varieties to be used in the best growing areas. However, the trial did show that a selection of phormium could be grown at this location. The economics of production were not investigated.

TABLE 12.—*Yield indexes of phormium introductions at three Oregon locations*

Location and selection No.	Average yield index	Rank [1]
Medford:		
P5–1–1	[2] 7, 296	A
P3–1–5	6, 861	AB
P1–1–2	3, 721	BC
P4–1–14	2, 051	C
Coquille:		
P4–3–3	2, 036	A
P6–3–1	1, 936	AB
P2–3–1	1, 480	ABC
P3–1–17	1, 286	ABCD
P3–1–18	1, 202	ABCD
P6–3–5	1, 136	ABCD
P1–G	1, 118	BCD
P2–3–13	1, 038	BCD
P6–3–17	926	CD
P3–1–14	786	CD
P2–3–15	628	CD
P2–1–13	576	CD
P4–1–3	500	D
Camp Adair:		
P1–2–5	700	A
P1–2–13	674	AB
P4–4–17	388	ABC
P6–4–9	365	ABC
P2–4–3	362	ABC
P2–2–13	330	BC
P4–4–19	290	C
P1–2–3	263	C
P4–4–1	208	C
P6–2–1	56	C

[1] Duncan's Multiple Range Test, $P = 0.05$. Treatments with same letters are not significantly different.

[2] Units for the Medford trial are in pounds fiber per acre rather than a yield index.

Seed Germination

Smerle (*25*) in 1927 and Toole [7] in 1954 reported that seeds of *P. tenax* germinated slowly. Toole found that one sample of phormium seeds germinated 92 percent after 402 days of incubation at a 15° to 25° C. temperature alternation. Seeds were considered dormant for an undetermined time after harvest. The 15° to 25° daily temperature alternation was not sufficient to bring about complete germination of such seeds. Stratification did not result in any beneficial effect.

For germination studies, seed pods of variety P4 were collected from Brookings in 1957 and seeds were selected for each treatment. Differences in seed size were not

[7] TOOLE, E. H. U.S. Department of Agriculture. 1954. [Mimeographed.]

considered; seeds with no embryos were discarded. Each treatment included 200 seeds sown on moistened paper towelling in 4 petri dishes, each containing 50 seeds.

Tests were conducted at constant temperatures of 5°, 10°, 15°, 20°, and 30° C. and at daily temperature alternations (16 hours at lower temperature in the dark, and 8 hours at higher temperature with light) of 15° and 25°, 15° and 30°, and 20° and 30°. Germination counts were made each week. Seeds showing emergence of the radicle from the seed coat were considered to be germinated. Results are shown in figure 14. The germination rate was high in the early period of incubation in the case of the alternating temperatures of 15° and 30°, but mold growth was higher then than at 15° and 25°.

The effects of chemical treatment on seed germination were also studied. Seeds of variety P4 and the Wollam clone, all of which had been stored in plastic bags at 3° C. for 1 year, were used.

Seed lots each containing 200 seeds were selected at random and subjected to the following treatments:

Soaked for 24 hours in:
- (1) 5 percent thiourea (10 cc.),
- (2) 0.25 percent thiourea (10 cc.),
- (3) 1 percent hydrogen peroxide, and
- (4) 1.5 percent hydrogen peroxide.

Soaked for 20 minutes in:
- (1) 2.5 percent Clorox and
- (2) 2.5 percent Clorox and then soaked for 24 hours in 3 percent hydrogen peroxide.

Dusted lightly or coated with Methocel, then dusted with one of the following fungicides: Arasan, Spergon, Semesan, Ceresan, or Orthocide 75 plus Captan 75.

After the seeds were treated, they were placed on moistened paper toweling in petri dishes and subjected to 15° C. temperature for 16

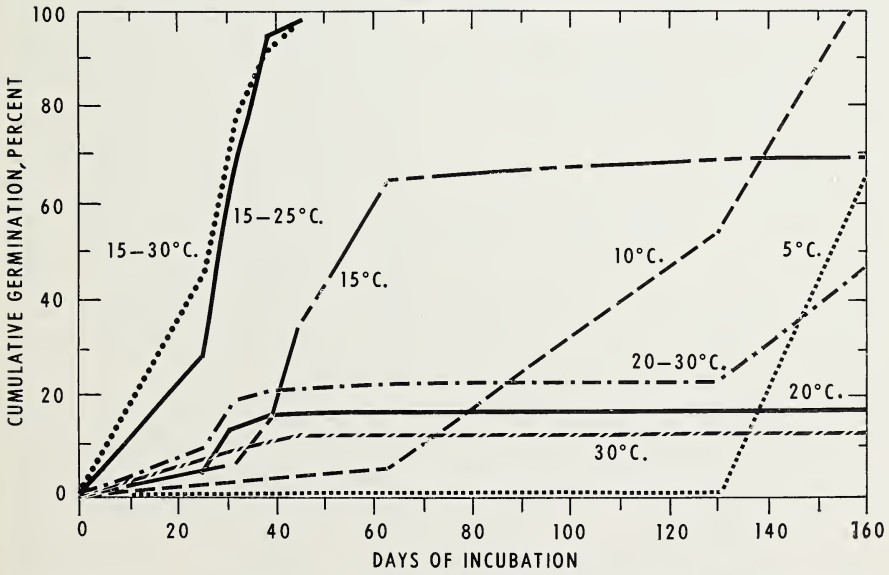

FIGURE 14.—The effect of temperature on the germination of fresh seeds of *P. tenax* variety P4.

hours in the dark and 25° C. for 8 hours in the light.

Germination counts were made weekly to evaluate the effects of these treatments on seed germination. Fungus or mold on the seeds and on the paper toweling was observed and recorded.

Chemical treatment did not increase germination. After 45 days of incubation, germination was highest in untreated seeds—61 percent in P4 and 63 percent in the Wollam clone. After 30 days of incubation, germination of P4 seeds treated with 1.5 percent hydrogen peroxide was 57 percent. Germination of P4 seeds treated with 2.5 percent Clorox was only 8.5 percent after 17 days of incubation but was 57 percent after 30 days. Further studies should be conducted on the effects of chemicals and other seed treatment methods on seed germination.

There was no mold growth on the seeds or paper toweling when the seeds were dusted lightly with Arasan.

Reciprocal crosses were made between the plants of different genotypic origins at Brookings and Gold Beach in 1958 to study the effects of hybridization on seed germination. Forty hours after emasculation, flowers were pollinated with 18-hour-old pollen. In addition, some emasculated flowers were pollinated by hand with the 18-hour-old pollen from the same flower stalk.

Seed pods were collected 70 days after anthesis. Open-pollinated seeds were collected when the pods were about to shatter. Seed pods were threshed by hand immediately and allowed to germinate in petri dishes in moist sand.

In some cases, speed of initial and total germination of seeds increased or decreased when two parents were combined. Self-pollination reduced seed germination. The effects of hybridization on seed size, seed germination, and seedling vigor of *P. tenax* should be studied further.

Seed Maturity

Twenty flower stalks were selected from a phormium field at Gold Beach in 1957 for studies of the effects of seed maturity on seed size, moisture content, cumulative germination, and seedling vigor (table 13). Not enough flower stalks from one variety were available, so flower stalks from other varieties were included. For subsequent seed germination and seedling vigor studies, however, seeds from only one plant were used.

Flowers were tagged at the beginning of anther exsertion. The date of flowering was marked on the tags. Seed pods were collected from these flower stalks 38, 59, 71, 84, and 90 days after anthesis.

After each collection, the seed pods were kept in a plastic bag until they were threshed by hand. The procedure used to evaluate maturity effects was as follows:

(1) 100 seeds were dried for 24 hours at 85° C. in a forced-air oven, and moisture contents of the seeds were calculated on a wet weight basis (table 13) as an indication of seed size and food reserve.

(2) Other seeds were allowed to air dry for 6 hours at room temperature. Two hundred seeds were counted at random, dusted with Arasan, and spaced uniformly on moist paper toweling in 4 petri dishes, each containing 50 seeds. These seeds were incubated at a daily temperature alternation of 15° and 25° C.

(3) Seeds which showed emergent radicles were considered to be germinated. After a daily count, germinated seeds were transferred to another dish containing moist paper toweling for further growth. Dates of emergence were recorded on the moist paper toweling with an indelible pencil.

TABLE 13.—*Effects of seed maturity on seed size, moisture content, seed germination, and seedling vigor indices of phormium*

Location, year, and days after anthesis	Seed size (Dry weight—100 seeds)	Moisture content (Wet weight basis)	Cumulative germination				Seedling vigor indices	
			Total	Incubation interval	30 days	45 days	Seedling length	Root length
Gold Beach, 1957:	*Milligrams*	*Percent*	*Percent*	*Days*	*Percent*	*Percent*	*Centimeters*	*Centimeters*
38	186	79	55	109	5	13	4.5	1.5
59	581	55	92	60	37	75	8.0	2.9
71	820	47	99	53	59	96	11.6	5.8
84	804	23	99	53	84	97	11.8	5.9
90	808	20	98	53	78	97	12.5	6.3
Brookings, 1958:								
20	[1]							
35	344	80	[2]					
50	522	55	11	88	9	11	3.9	1.9
65	648	46	69	88	35	58	8.9	5.1
80	668	33	67	88	40	63	9.5	4.9
95	737	22	71	88	55	66	9.0	4.9
110	653	10	53	88	36	46	10.5	4.8

[1] Milky; seed did not germinate.
[2] Seed coat was hard and black, but seed did not germinate.

(4) Dishes containing seedlings were checked daily for moisture and fungus growth. Throughout the study, the paper toweling was kept saturated with water. In case any fungus growth appeared in the dish, the seedlings were transferred to another dish containing new moist paper toweling. Each seedling was taken out of the dish after growing 22 days, and the following observations were made on each seedling for seedling vigor indices:

(a) Seedling length from root tip to shoot tip (table 13).[8]
(b) Root length from root tip to the intersection of root and shoot (table 13).
(c) Total green or fresh weight of seedling plus seed coat.
(d) Fresh or green weight of seedling and seed coat separately.
(e) Total dry weights of seedling plus seed.
(f) Dry weight of seedling.
(g) Dry weight of seed coat.

(5) Seedlings were dried in weighing bottles in an oven at 89° C. When the seedlings reached a constant weight, they were transferred to a desiccator containing calcium chloride. The seedlings were weighed after the material had cooled for 10 minutes.

In 1957, from 50 to 150 seedlings from each stage of maturity (days after anthesis) were tested for vigor. In 1958, 25 flower stalks were selected at random from the Wollam clone at Brookings. Seed pods were collected from these flower stalks 20, 35, 50, 65, 80, 95, and 110 days after anthesis. Other procedures in 1958 were similar to those used in 1957. Results are given in table 13.

In 1957, at Gold Beach, the dry weight of seeds increased linearly with each increment of maturity up to 71 days (table 13). After 71 days, the dry weight of the seeds decreased. In 1958, at Brookings, the dry weight of the seeds also increased linearly with each increment of maturity until 95 days. Dry weights were lower in seeds harvested after 110 days, than in those harvested after 95 days.

Moisture content of the seeds decreased rapidly with each increment of maturity. In 1957, the moisture content of the seeds after 71 and 84 days was 47 and 23 percent, respectively. In 1958, the moisture content of the seeds after 95 days was 22 percent. The moisture content was only 10 percent in seeds harvested 110 days after anthesis. Some of the seed pods had already shattered at this stage.

Weight of the seed coat increased markedly as seed matured in 1957, but increased only slightly in 1958. The seedlings from each treatment contained about the same amount of moisture each year. The difference in moisture content of seedling and seed coat was 9.6 percent.

Germination and seedling vigor were directly proportional to seed weight and, therefore, to the amount of food reserve present in the seed or seed coat.

In another test, a seed lot of the Wollam clone was collected from Brookings in 1957 at the shattering stage of the seed pod (table 14). Seeds were dried in a room at 75° F. with a relative humidity of 50 percent, then stored in plastic bags at 3° C. The moisture content of each seed lot was determined by the oven method. The average moisture content at the time of storage was 8.6 percent on a dry weight basis.

Seeds of *P. tenax* of differing maturity levels were collected at Gold Beach in 1957 and stored in glass bottles with different moisture content levels at temperatures of 3° C. and −3° C.

Storage at 3° C. enhanced seed

[8] Length measures were in centimeters, weight in milligrams.

TABLE 14.—*Effects of maturity level, storage conditions, and moisture content on germination of phormium seeds, 1957*

Seed maturity level	Storage conditions		Moisture content (dry basis)	Germination		
	Time	Temperature		Before storage	After 25 days' incubation	After 60 days' incubation
Collected at random from field:	*Months*	*° C.*	*Percent*	*Percent*	*Percent*	*Percent*
At shattering stage (Wollam clone)	12	3	8.6	98	42	81
Not dried	10	−3	21.1	78	14	14
Dried	10	3	14.0	78	3	5
Stored at Corvallis	10	[1]	7.6	78	1.5	4
90 days' maturity:						
(1)	10	3	11.4	98	86	95
(2)	[2]		11.4	98	57	
(3)	10	−3	20.4	98	73	80
84 days' maturity	10	−3	27.5	99	73	80
71 days' maturity	10	−3		99	20	35
59 days' maturity	10	−3	35.5	92		

[1] Room temperature. [2] No storage.

germination. Eighty-six percent of the seeds of 90 days' maturity, which had been stored for 10 months at 3° C., germinated after 25 days of incubation, whereas only 57 percent of the fresh seeds germinated after 25 days. Perhaps the immature embryos matured during storage and thus increased the speed of germination. On this basis, dormancy due to immature embryo might be the reason for the slow germination. Other germination data are in table 14.

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